Maintien de l'ornementation mutuelle chez le manchot royal (Aptenodytes patagonicus)

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Titre :
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Résumé :

Si la théorie de la sélection sexuelle proposée par Darwin fournit un cadre satisfaisant pour expliquer l'évolution et le maintien des ornements sexuellement dimorphiques, le cas de l'ornementation mutuelle requiert l'emploi du cadre plus large offert par la sélection sociale. Dans de nombreux cas en effet, l'explication du maintien de l'ornementation mutuelle nécessite de considérer non seulement la compétition pour l'accès au partenaire de reproduction, mais également la compétition pour l'accès à d'autres types de ressources telles que la nourriture ou les emplacements pour nicher.

Cependant, le maintien de l'ornementation mutuelle n'est encore que partiellement compris chez les oiseaux marins. Les travaux réalisés au cours de cette thèse s'inscrivent dans la continuité des recherches initiées depuis quelques années dans le but de comprendre le maintien de l'ornementation mutuelle chez le manchot royal, un oiseau exprimant un patch orange présentant un pic de réflectance ultraviolet de chaque côté de la mandibule, des patches auriculaires jaunes de chaque côté de la tête et un patch formant un dégradé allant du marron au jaune pâle sur le poitrail. Les travaux présentés dans ce manuscrit de thèse portent (i) sur les combats entre individus du même sexe pour accéder à un partenaire de reproduction, (ii) sur le rôle des ornements colorés dans le processus d'appariement, (iii) sur l'association entre le degré de développement des ornements et la position du territoire occupé au sein de la colonie, et enfin (iv) sur l'existence de variations interannuelles concernant le degré de coloration des ornements et le processus de choix de partenaire. Les résultats révèlent que : (i) les affrontements pour l'accès au partenaire sont beaucoup plus fréquents chez les mâles que chez les femelles ; (ii) l'ornementation mutuelle du bec pourrait être maintenu pas le processus de choix mutuel ; (iii) les individus occupant les territoires les plus centraux de la colonie expriment des patches auriculaires plus large et un patch de poitrine plus coloré ; (iv) les ornements présentent des variations notables entre deux années, tout comme le processus de choix de partenaire. Pris dans leur ensemble, ces résultats révèlent que le maintien de l'ornementation mutuelle du manchot royal est multifactoriel, et des pistes de recherches sont proposées pour affiner notre compréhension de ce phénomène complexe.

Mots clés : écologie comportementale, sélection sociale, sélection sexuelle, ornements colorés, *Aptenodytes patagonicus*

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Title:
Maintenance of mutual ornamentation in the king penguin (*Aptenodytes patagonicus*)

Abstract :

Darwin devised sexual selection theory in order to explain the evolution and maintenance of secondary sexual traits. In mutually ornamented species, however, the broader theoretical framework of social selection is needed. In many cases indeed, understanding the maintenance of mutual ornamentation requires to take into account competition for both sexual (i.e. mates) and non-sexual resources (e.g. food, nest sites).

How mutual ornaments maintain and evolve is actually not well understood in seabirds species. The aim of the research program within which this Ph.D. thesis took place was to understand the maintenance of mutual ornamentation in king penguin, a bird exhibiting a ultraviolet and orange beak spot on each side of the mandible, two yellow auricular patches, and a patch on the breast that grade from brown to bright yellow. We studied (i) same-sex fight over mates; (ii) mate choice for color ornaments; (iii) the relationships between conspicuousness of ornaments and position of the territory within the colony; and finally (iv) the existence of inter-annual variations in color ornaments expression and mate choice process. Our results show that: (i) same-sex fights over mates are highly male-biased; (ii) color of the beak spots may be involved in mutual mate choice; (iii) central individuals exhibit larger auricular patches and more colorful breast patch; (iv) ornament conspicuousness as well as mate choice show inter-annual changes. Taken together, these results reveal that maintenance of king penguin mutual ornaments is multifactorial, and some research avenues are suggested for future researches.

Key words: behavioral ecology, social selection, social selection, color ornaments, *Aptenodytes patagonicus*

TABLE DES MATIERES

1. Introduction

1.1. Contexte général

Les comportements sociaux tiennent une place importante dans la théorie de l'évolution (Darwin 1859, 1871 ; West-Eberhard 1979, 1983). Dans leur diversité et leur complexité, tous reposent sur des interactions mettant en jeu un transfert d'information entre un individu émetteur et un individu récepteur. Dans son acceptation stricte, la communication consiste en un transfert d'information par un émetteur via des structures ou des comportements qualifiés de *signaux*, dont la *fonction adaptative* est de modifier le comportement d'un ou plusieurs récepteurs. En d'autres termes, les deux parties tirent un avantage de la transmission d'information : l'émetteur à travers la modification du comportement du récepteur, et le récepteur à travers l'acquisition d'une information fiable (Théry & Heeb 2007).

La fiabilité des signaux est une question centrale en communication animale, et différents mécanismes peuvent être à l'œuvre selon le système étudié. Dans le cadre de cette thèse, nous ne présenterons que les mécanismes relatifs à la transmission d'information sur la qualité et /ou l'aptitude au combat des individus (voir Maynard Smith & Harper p. 6-9). Le premier est le *principe du handicap* proposé par Zahavi (1975, 1977), selon lequel la fiabilité l'information transmise est assurée par le coût de production du signal. Ainsi lorsque le signal transmet une information relative à la qualité de l'émetteur ou à son aptitude au combat, ce signal ne pourra être pleinement exprimé que par les individus de meilleure qualité. Le second mécanisme concerne les signaux qui ne peuvent être truqués, en raison de contraintes physiques. C'est le cas par exemple pour le brame du cerf élaphe (*Cervus elaphus*), dont les caractéristiques acoustiques sont contraintes par la taille du mâle (*indice of quality* : Maynard Smith & Harper 2003, p.45-46). Selon le canal de communication employé, les signaux peuvent être olfactifs (ex. Bonadonna & Sanz 2012), acoustiques (ex. Lengagne et al. 1999), ou visuels (ex. Jones & Hunter 1999). Les signaux visuels, de par l'extravagance et la diversité de leurs formes ont toujours suscité enthousiasme et intérêt de la part des biologistes.

1.1.1. Les structures extravagantes et la sélection sociale

Des bois du cerf élaphe aux plumes ornementales du paradisier de Lawes (*Parotia lawesii*), de nombreuses espèces animales présentent des traits morphologiques dont l'extravagance trouve son origine dans la compétition entre conspécifiques pour l'accès aux *ressources* (Darwin 1871 ; Andersson 1994 ; Tobias et al. 2012).

Les ressources désignent l'ensemble des éléments -biotiques ou abiotiques- indispensables au cycle biologique d'un individu mais présents en quantité limité dans un environnement donné, comme la nourriture, les emplacements pour nicher, ou encore les partenaires de reproduction. En conséquence de cette limitation, l'exploitation d'une ressource particulière par un individu donné réduit sa disponibilité pour le reste de ses congénères et le phénomène de compétition entre rivaux émerge (Giraldeau 2007). Cette compétition pour l'accès aux ressources est génératrice d'interactions sociales d'où émerge le processus évolutif de *sélection sociale*, concept initialement proposé par Crook (1972) puis théorisé par West-Eberhard (1979, 1983 ; voir également Lyon & Montgomerie 2012 ainsi que Tobias et al. 2012). La sélection sociale peut être définie comme un processus de tri entre variants phénotypiques d'une même espèce, se faisant sur la base de différences héritables dans leur capacité à accéder aux ressources nécessaires à leur survie et à leur reproduction dans un contexte d'interactions entre conspécifiques. Ainsi, au sein d'une population, tout trait présentant une héritabilité non nulle et améliorant la valeur sélective de son porteur lorsque ce dernier interagit avec ses conspécifiques augmentera en fréquence au cours des générations (West-Eberhard 1979, 1983 ; Moore et al. 1997 ; Wolf et al. 1999 ; McGlothlin et al. 2010). Si les caractères extravagants revêtent une grande diversité de formes à travers le règne Animal, la prise en compte du contexte social dans lequel ils trouvent leur fonction permet de les classer en trois grandes catégories : les armements, les ornements, et les badges de statut.

Les *armements* désignent l'ensemble des traits ayant pour fonction d'influencer l'issue d'une interaction agonistique entre individus, par exemple lors des combats entre mâles chez le cerf élaphe pour l'accès aux harems de femelles lors de la période de rut (Clutton-Brock et al. 1982). Souvent, ces structures jouent le rôle de révélateurs de l'aptitude au combat de leur porteur et le combat réel ne se produit qu'entre individus dont les armements présentent un degré de développement semblable ; lorsque l'asymétrie entre deux rivaux potentiels est trop importante, le conflit n'escalade pas jusqu'au contact physique (Clutton-Brock et al. 1982 ; Bergeron et al. 2010 ; une revue récente de l'évolution des armements pourra être trouvée dans Emlen 2008). Les *ornements* désignent l'ensemble des traits exprimés par une catégorie

d'individus et ayant pour fonction d'influencer le choix exprimé par les individus d'une catégorie différente. La situation la plus connue est celle du choix de partenaire ; chez le paradisier de Lawes par exemple, les femelles s'accouplent préférentiellement avec les mâles exprimant les plumes ornementales les plus développées (Pruett-Jones & Pruett-Jones 1990 ; voir Andersson 1994 pour une revue exhaustive des travaux empiriques ayant trait au choix de partenaire dans le règne Animal, ainsi que Hill 2006 et Amundsen & Parn 2006 pour des revues focalisées sur les oiseaux). Une autre situation est celle du nourrissage préférentiel de certains membres d'une progéniture par leurs parents : chez la foulque d'Amérique *Fulica americana*, il a ainsi été observé que les poussins les plus colorés bénéficiaient d'un apport en nourriture plus important de la part de leurs parents (Lyon et al. 1994). Les *badges de statut* peuvent être définis comme des structures impliquées dans la médiation des interactions agonistiques, et se présentent sous la forme de patches colorés (incluant le noir) où de plumes allongées (Maynard Smith & Harper 2003). Chez le souimanga de Johnstone (*Nectarinia johnstoni*) par exemple, un passereau au plumage de couleur verte iridescente présentant des patches pectoraux écarlates, il a été observé que les individus dont les patches avaient été expérimentalement agrandis subissaient moins d'agressions de la part de la part de leurs congénères et arrivaient à occuper et défendre des territoires plus riches en ressources, tandis que l'opposé se produisait chez les individus pour lesquels les patches avaient été rétrécis (Evans & Hatchwell 1992).

Notons toutefois que dans certain cas, la frontière entre armements, ornements, et badges de statut est floue. Chez le mouflon canadien (*Ovis canadensis*) par exemple, les cornes des mâles jouent le rôle d'armement, mais leur degré de développement fait également l'objet d'un choix de la part des femelles (Geist 1971, cité dans Berglund et al. 1996). De la même manière, les badges de statut peuvent être rapprochés tant des armements que des ornements : *armements* dans le sens où même s'ils ne peuvent infliger de blessures, ils influencent malgré tout l'issue d'un conflit ; et *ornements* dans la mesure où ils peuvent, en plus d'influencer l'issue d'un conflit entre mâles, faire l'objet d'un choix de la part des femelles (voir le concept des *traits à double utilité* développé par Berglund et al. 1996). La suite de ce manuscrit se focalise sur les oiseaux, et le terme d'*ornement* sera employé pour désigner à la fois les badges de statut et les structures extravagantes impliquées dans les processus de choix.

1.1.2. La sélection sexuelle et l'ornementation mutuelle

En partant du constat que les mâles de nombreuses espèces animales présentent un degré d'ornementation supérieur à celui des femelles, Darwin (1871) s'est attaché à comprendre l'évolution et le maintien d'un tel dimorphisme en se focalisant sur l'étude de la compétition entre mâles pour l'accès aux femelles, compétition à l'origine du processus évolutif de *sélection sexuelle* (Darwin 1859, 1871 ; voir également Lyon & Montgomerie 2012 ainsi que Tobias et al. 2012). Dans le cadre de la sélection sexuelle, l'investissement de chaque sexe dans la production d'ornements favorisant l'acquisition de partenaires de reproduction dépend de l'avantage qui en est tiré en termes de production de descendants. Cet avantage dépend en grande partie de l'investissement parental, souvent plus important chez les femelles (Trivers 1972). Chez les espèces où les soins parentaux sont exclusivement assurés par les femelles par exemple, un mâle peut s'accoupler avec plusieurs femelles dans un laps de temps très court, tandis qu'une femelle ne peut s'accoupler avec un nouveau mâle qu'une fois sa progéniture devenue indépendante. Il émerge ainsi une asymétrie entre les sexes, selon laquelle les femelles disposent de plus d'opportunités d'accouplement qu'elles ne peuvent en réaliser tandis que les mâles ne disposent que d'un nombre limité d'opportunités par rapport à ce qu'ils peuvent accomplir. Chez les femelles ce contexte favorise l'évolution et le maintien d'un certain degré de discrimination parmi l'ensemble des partenaires potentiels afin de ne s'accoupler qu'avec les meilleurs, tandis que chez les mâles ce contexte favorise l'évolution et le maintien d'ornements extravagants ayant pour fonction d'accroitre leur probabilité d'être choisis comme partenaire (par exemple chez le Paradisier de Lawes : Pruett-Jones & Pruett-Jones 1990). D'une manière générale, la théorie de la sélection sexuelle fournit un cadre explicatif à l'évolution et au maintien du dimorphisme sexuel satisfaisant, tant sur le plan empirique que sur le plan théorique (Andersson 1994 ; Kokko & Johnstone 2002 ; Griffith & Pryke 2006 ; Hill 2006 ; Kokko & Jennions 2008 ; Kokko et al. 2012).

Chez un certain nombre d'espèces les mâles et les femelles sont ornementés (voir Kraaijeveld et al. 2007 ainsi que Tobias et al. 2012 pour des revues récentes), et le processus de *choix mutuel du partenaire* a été proposé (Huxley 1914) pour expliquer l'évolution et le maintien de cette ornementation mutuelle. Selon une récente formalisation théorique, ce choix mutuel est attendu chez les espèces présentant un taux de rencontre entre partenaires potentiels élevé, un coût de recherche du partenaire faible, et un investissement parental élevé et de même magnitude chez les deux sexes (Kokko & Johnstone 2002). Ces caractéristiques sont retrouvées chez les oiseaux marins : en tant que reproducteurs coloniaux (Danchin & Wagner 1997) ils ont l'opportunité d'évaluer un nombre important de partenaires potentiels

dans espace relativement restreint (la colonie), les soins biparentaux sont obligatoires et s'étendent souvent sur plus de six mois pour assurer la survie de la couvée (composée d'un seul œuf dans de nombreux cas ; Schreiber & Burger 2002). L'hypothèse du choix mutuel du partenaire a été testée chez plusieurs espèces d'oiseaux marins mutuellement ornementé et jouit d'un certain support (starique minuscule *Aethia pusilla*: Jones & Montgomerie 1992; starique cristatelle *Aethia cristatella*: Jones & Hunter 1993; sterne inca *Larosterna inca*: Velando et al. 2001; grand cormoran *Phalacrocorax carbo*: Childress & Bennun 2002; cormoran huppé *Phalacrocorax aristotelis*: Daunt et al. 2003; manchot antipode *Megadyptes antipodes*: Massaro et al. 2003; fou à pieds bleu *Sula nebouxii*: Torres & Velando 2003, 2005; manchot royal *Aptenodytes patagonicus*: Pincemy et al. 2009, Nolan et al. 2010; sterne de Dougall *Sterna dougallii*: Palestis et al. 2012).

1.2. L'étude de l'ornementation mutuelle chez le manchot royal

A l'instar de la majorité des oiseaux marins, le manchot royal est un reproducteur colonial. Son cycle reproducteur est particulièrement long, et chaque couple requiert entre 14 et 16 mois pour élever son unique poussin avec succès (Stonehouse 1960 ; Weimerskirch 1992 ; Descamps et al. 2002 ; figure 1). Au sein de chaque sexe donc, le succès reproducteur sera pour une grande partie déterminé par la qualité du partenaire acquis. Ajouté à cela, le taux de divorce interannuel est estimé à 63% (Toscani et al. en préparation) et une majorité d'individus doit donc trouver un nouveau partenaire à chaque nouvelle saison. Ces deux premiers éléments suggèrent que le processus de choix mutuel est être à l'œuvre, et qu'il pourrait jouer un rôle dans le maintien de l'ornementation mutuelle observée chez cette espèce (Kokko & Johnstone 2002 ; Kraaijeveld 2003). De plus, les colonies de manchots royaux sont extrêmement denses, et chaque couple occupe un territoire d'environ 0.5 m^2 (Barrat 1976) dont la qualité varie en termes d'exposition à la prédation, aux inondations, et aux parasites (Descamps et al. 2009). Dans le cadre de la sélection sociale, ces deux éléments suggèrent qu'un certain degré de compétition pour l'accès à un territoire de qualité devrait être à l'œuvre, et favoriser le maintien d'ornements colorés conférant à leurs porteurs un avantage dans l'issue des interactions agonistiques résultant de cette compétition (West-Eberhard 1979, 1983). Enfin, durant toute la durée du cycle reproducteur les séjours à terre se caractérisent par de fréquentes interactions agonistiques, notamment lors de la période de formation des couples (voir plus bas).

De tous ces éléments, il ressort que le maintien de l'ornementation mutuelle du manchot royal est potentiellement sous tendu par un ensemble complexe d'interactions directes et indirectes (c.à.d. combats et choix, respectivement) pour l'accès au partenaire et au territoire. Les travaux réalisés dans le cadre de cette thèse visent à améliorer notre compréhension de ce maintien.

1.2.1. Le cycle reproducteur du manchot royal

Le cycle reproducteur du manchot royal dure en moyenne 14 mois et débute avec le printemps austral (figure 1). Les individus commencent par former des groupes de mue, et acquièrent le nouveau plumage au bout de 23 jours. Ils retournent ensuite en mer pendant environ 2 semaines, et reconstituent leurs réserves énergétiques en allant se nourrir au front polaire (Charrassin & Bost 2001). Cette étape est particulièrement importante pour les mâles (Gauthier-Clerc et al. 2001 ; voir plus bas). Au retour de ce voyage en mer, les individus entament le processus de formation des couples : il consiste en l'émission de chants (porteurs d'une signature individuelle : Derenne et al. 1979) et la réalisation de parades ritualisées (Jouventin 1982). A ce moment des interactions agonistiques prenant la forme de trios sont fréquemment observées, semblables à celles observées chez le manchot empereur *Aptenodytes forsteri* : deux individus de même sexe s'affrontent pour accéder à un partenaire de reproduction (Prévost 1961; Mougin 1966; Jouventin et al. 1979). Lorsqu'un couple est formé, il acquiert un territoire : lors de cette acquisition, de nombreuses interactions agonistiques sont également observées. Quelques jours après l'établissement du territoire la femelle pond l'œuf, le mâle le récupère et le cycle d'incubation commence. Après la ponte, la femelle retourne en mer afin de reconstituer ses réserves énergétiques ; le mâle, lui, continue de jeuner. Si le mâle ne dispose pas de réserves énergétiques suffisantes et que sa masse descend en dessous d'un seuil critique avant le retour de la femelle, il abandonne l'œuf (Gauthier-Clerc et al. 2001). Le cycle d'incubation dure 54 jours, au cours desquels les parents se relaient tous les 10 à 15 jours en moyenne, et les premières éclosions sont observées fin janvier (Stonehouse 1960 ; Weimerskirch et al. 1992 ; Descamps et al. 2002). Un mois après l'éclosion, les poussins atteignent l'émancipation thermique et commencent à former des crèches. Les poussins continuent d'être nourris par les deux parents jusqu'à la fin de l'été austral. A partir de mi-Mai, les parents retournent en mer pour se nourrir dans la zone marginale des glaces (Charrassin & Bost 2001). Durant l'hiver austral, les visites des parents aux poussins sont rares, et ces derniers supportent des périodes de jeun dont la durée moyenne oscille entre 50 et 100 jours (Saraux et al. 2012). Le taux de mortalité hivernal des poussins

est très changeant selon les colonies et les années, et peut varier entre 60 et 99 % (Weimerskirch et al. 1992). Lorsque le printemps austral de l'année suivante commence, les parents retournent à la colonie et finissent d'élever leur poussin si celui-ci a survécu. L'élevage prend fin aux alentours du mois de décembre. Les individus réussissant à élever un poussin avec succès entament donc leur nouveau cycle reproducteur beaucoup plus tard ; en conséquence, le poussin qu'ils engendreront lors de cette nouvelle année aura très souvent accumulé trop peu de réserves énergétiques avant l'arrivée du nouvel hiver austral, et n'y survivra pas (Weimerskirch et al. 1992).

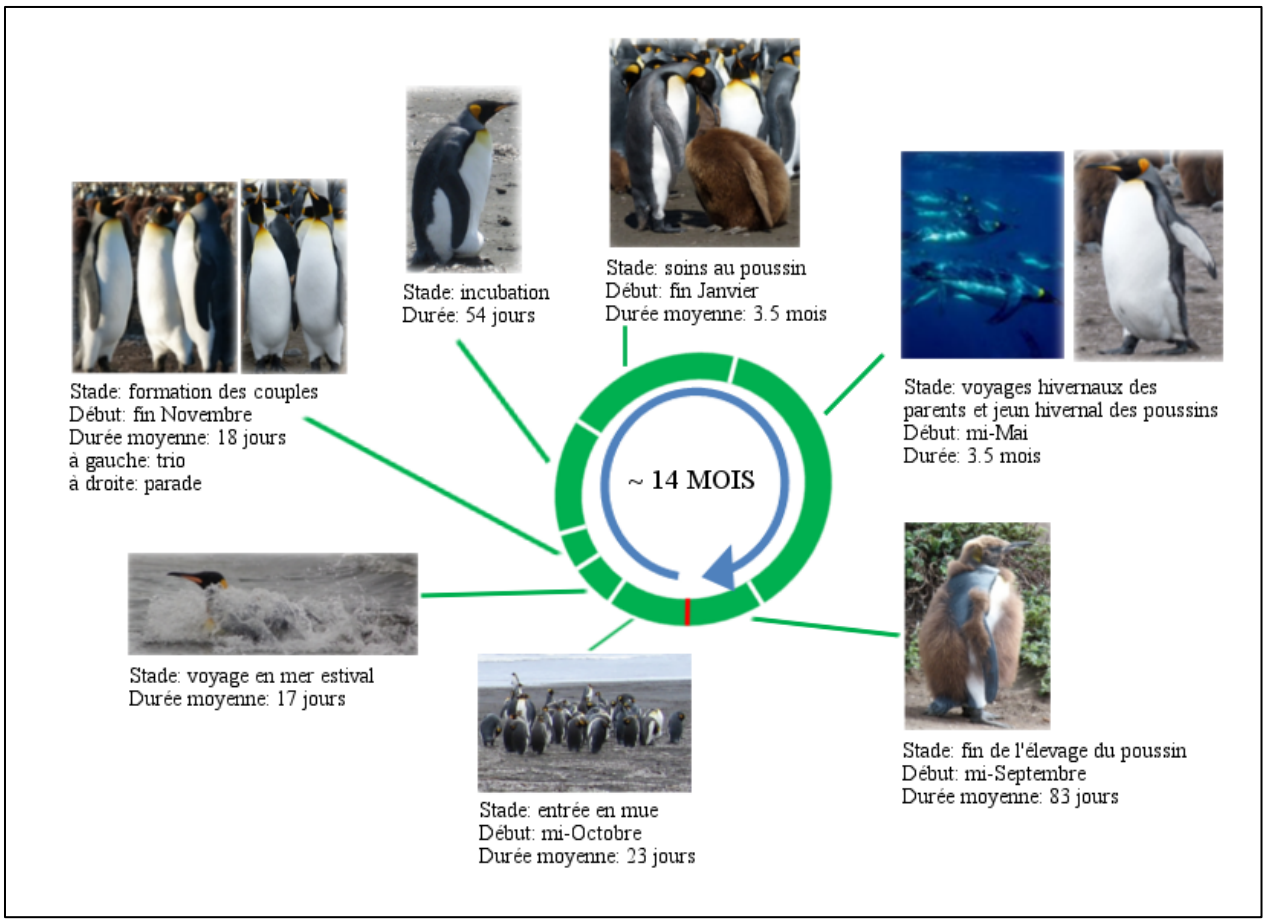

Figure 1. Cycle reproducteur du manchot royal. Le marqueur rouge indique le point de départ, au début du printemps austral. D'après Stonehouse (1960), Wermerskirch et al. (1992), et Descamps et al. (2002). Photographie sous-marine : D. Beaune ; autres photographies : I. Keddar.

1.2.2. Les ornements du manchot royal

Le manchot royal possède trois type d'ornements : de chaque côté de la mandibule se trouvent deux patches orange présentant un pic de réflectance dans l'ultraviolet, entre la gorge et la partie supérieure du poitrail s'étend un dégradé allant du marron au jaune pâle, et sur la tête deux patches auriculaires de couleur jaune-orange sont observés (figure 2). Ces patches auriculaires sont plus larges chez les males que chez les femelles (Dobson et al. 2011). La coloration des plumes résulte de la présence d'un pigment propre à la famille des Sphéniscidés et dont la structure est proche des ptérines (McGraw et al. 2004 ; McGraw et al. 2007 ; Thomas et al. 2013). Les patches de la mandibule, quant à eux, sont de nature composite : le pic de réflectance ultraviolet est structural (Jouventin et al. 2005 ; Dresp et al. 2005 ; Dresp & Langley 2006), tandis que la coloration orange résulte de la présence de caroténoïdes (McGraw et al. 2007).

Ces trois ornements ont été principalement étudiés sous l'angle du choix de partenaire. Chez les deux sexes, une altération de la réflectance UV du bec par l'application d'un vernis entraine un délai dans l'acquisition d'un partenaire. De plus, chez les mâles uniquement, la réduction expérimentale de la taille des patches auriculaires (Jouventin et al. 2008 ; Pincemy et al. 2009 ; Nolan et al. 2010) ainsi que l'altération de la couleur des patches auriculaires ou du dégradé du poitrail entraine un délai dans l'acquisition d'une femelles (Pincemy et al. 2009). Concernant la défense du territoire, une étude corrélative rapporte que les individus exprimant les patches auriculaires les plus larges sont les plus agressifs et occupent les territoires les plus centraux de la colonie, moins exposés aux prédateurs ; le rôle de la couleur des ornements, toutefois, n'a pas été exploré (Viera et al. 2008).

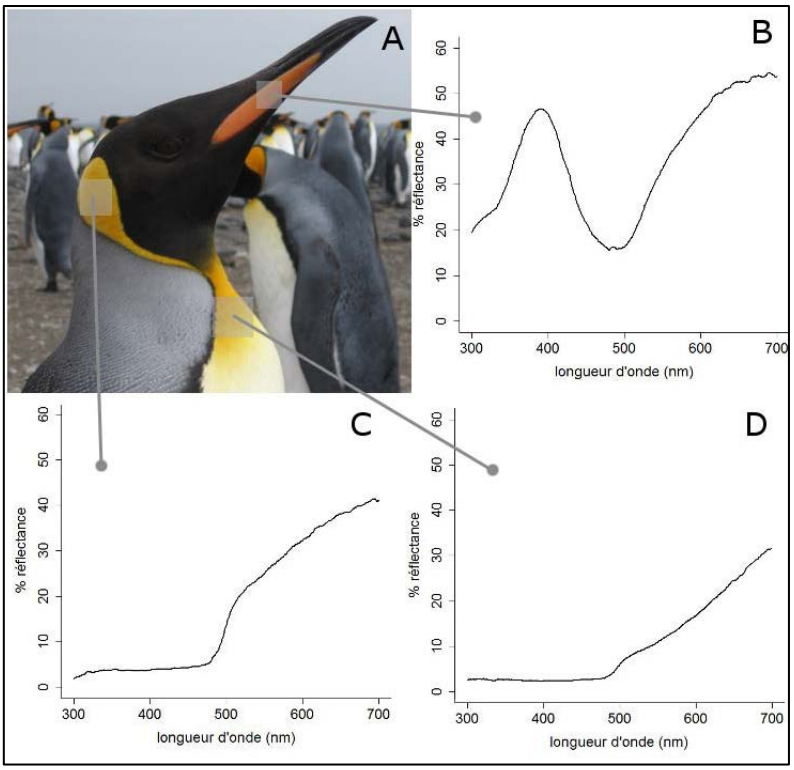

Figure 2. (A) Ornements colorés du manchot royal et (B) spectre de réflectance du bec, (C) spectre de réflectance du patch auriculaire, et (D) spectre de réflectance du patch de poitrine correspondants. Photographie : I. Keddar.

1.3. Présentation succincte des manuscrits d'articles

Les travaux réalisés au cours de cette thèse s'inscrivent dans la continuité d'un projet à long terme visant à comprendre le maintien de l'ornementation mutuelle chez le manchot royal. Ce manuscrit de thèse comporte quatre manuscrits d'articles, chacun constituant un chapitre. Le premier traite des trios observés au début de la période de formation des couples. L'objectif de cette étude est d'obtenir une approximation qualitative de l'intensité de la sélection à laquelle chaque sexe est soumis, en comparant les fréquences relatives auxquelles les trios impliquant des affrontements entre mâles d'une part, et entre femelles d'autre part, sont observées. Ce chapitre a été publié dans le journal Ethology (volume 119, p. 389-396). Le second chapitre traite du choix de partenaire et vise à éclairer le rôle joué par les couleurs ornementales dans le processus d'appariement. Cette question a été abordée sous un aspect expérimental par le passé, mais les modifications de couleurs ont été en partie réalisées en dehors de la gamme de variation naturelle des ornements (Pincemy et al. 2009 ; Nolan et al. 2010). Dans le cas de notre étude, les couleurs n'ont pas été altérées. Ce chapitre a été soumis

au journal Animal Behaviour et rejeté. Une critique émise par les deux évaluateurs du manuscrit concerne la méthode utilisée pour décrire et quantifier les couleurs ornementales ; ce point particulier est détaillé et discuté dans la dernière partie de ce manuscrit de thèse (chapitre 7). Le troisième chapitre traite du lien entre la couleur des ornements et la qualité du territoire occupé. Le quatrième chapitre est une comparaison interannuelle du degré d'expression des ornements colorés et du choix de partenaire. Ces deux derniers manuscrits sont encore en préparation, et présentés dans leur état actuel d'avancement.

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2. Male biased mate competition in king penguin trio parades

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Darwin devised sexual selection theory to explain sexual dimorphisms. Further developments of the theory identified the operational sex-ratio (OSR) as one of its cornerstones, and it was commonly admitted that an OSR biased toward one sex would lead to stronger selection pressures toward that sex. Recent theoretical developments have challenged this view, and showed that the OSR alone does not determine the direction of sexual selection, more particularly in mutually ornamented species exhibiting high and similar parental investment by both sexes. These developments, however, focused on mutual intersexual selection, and little is known about intrasexual selection of both males and females in species exhibiting such characteristics. The first aim of our study was to test the relative involvement of males and females in same-sex contests over mates in the king penguin, a species exhibiting mutual ornamentation of the sexes, high parental investment by both sexes, and a male-biased OSR. We investigated the sex composition of trio parades, which are groups of three individuals that compete for mates during pair formation. We found that these trios consist of a female trailed by two fighting males in 19 of 20 cases; the 20th trio was all male. The second aim of our study was to investigate the existence of within-sex differences in colour ornaments between individuals involved in such trios and individuals already paired. While limited sample sizes precluded detection of statistically significant differences between trios versus pairs, reflectance measurements suggested that the beak spot of males in trios were more strongly ultraviolet than the beak spot of males in pairs. We concluded that intrasexual selection in our colony follows the typical pattern of mate competition observed in species in which sexual dimorphisms and OSR are male-biased, and discussed the ultraviolet difference within the framework of the king penguins' colour perception.

Keywords: *Aptenodytes patagonicus*, seabirds, same-sex contests, operational sex-ratio, mutual sexual selection

2.1. Introduction

Charles Darwin (1871) developed the theory of sexual selection to explain the evolution of secondary sexual traits. Such traits can be morphological, behavioural, or biochemical, and result from competition for reproductive advantages during the period when matings occur. Sexual selection can operate through two modalities, intrasexual selection and intersexual selection. Intrasexual selection involves interactions between individuals of the same sex, either before copulation (e.g. same-sex fights, scramble competition or endurance rivalry; reviewed in Andersson 1994) or after it (sperm competition; reviewed in Eberhard 2009). Intersexual selection involves interactions between males and females; here again, these interactions can be precopulatory (mate choice; Andersson 1994) or postcopulatory (cryptic female choice; Eberhard 2009).

A key concept to understand how secondary sexual traits can evolve by sexual selection is the *operational sex-ratio* (OSR), originally defined as the average ratio of fertilizable females to sexually active males at any given time (Emlen & Oring 1977). OSR, however, is now commonly defined reciprocally as the average ratio of males to females who are ready to mate in a population at a given time (Kvarnemo & Ahnesjö 1996; Kokko et al. 2012). As a ratio, any deviation from 1 means that one sex is more abundant than the other (males if OSR > 1, females if OSR < 1). When the OSR is biased toward a sex, individuals of that sex are expected to experience greater competition for mates than members of the non-limited sex, and thus traits that favour overcoming rivals may evolve. Examples of secondary sexual traits influencing the outcome of mate competition under intrasexual selection are armaments, such as antlers of male red deers *Cervus elaphus* (Clutton-Brock et al. 1982), sensory structures aimed at detecting sex pheromones under scramble competition, such as chemoreceptors on the pedipalps and forelegs of males of many spider species (reviewed in Gaskett 2007), body size to increase endurance rivalry, as suggested in males koala *Phascolarctos cinereus* (Ellis & Bercovitch 2011), or mate-guarding to prevent sperm competition (see Birkhead 1998 for a review of sperm competition in birds). Although all these examples deal with intrasexual selection in males, several studies reported intrasexual selection in females too (Kvarnemo & Ahnesjö 1996; Clutton-Brock 2009; Baldauf et al. 2011; Rosvall 2011; Tobias et al. 2012). Under intersexual selection, the sex experiencing a stronger competition due to mate limitation is expected to evolve secondary sexual traits aimed at influencing choice of the opposite sex, such as elaborate ornaments (e.g. tail length in the long-tailed widowbird *Euplectes progne*: Andersson 1982). Hence, a biased OSR seems

to lead to quite straightforward predictions about the strength of selection in males and females: traits that favour overcoming same-sex rivals should evolve primarily in the sex toward which the OSR is biased (reviewed in Kvarnemo &Ahnesjö 1996; Clutton-Brock 2009; Weir et al. 2011).

This view, however, has been challenged by a series of theoretical developments showing that the OSR alone does not determine the direction of sexual selection (Kokko & Monaghan 2001; Kokko & Johnstone 2002; Klug et al. 2010; Kokko et al. 2012). More particularly, if parental investments of both sexes are large and not too different from each other, mutual mate choice and mutual ornaments can evolve even under a highly biased OSR (Kokko & Johnstone 2002). Little is known, however, about mutual intrasexual selection in species exhibiting such characteristics (Rosvall 2011).

The first aim of our study was to test the relative involvement of males and females in same-sex contests over mates in the king penguin *Aptenodytes patagonicus*. The king penguin is a mutually ornamented species (Jouventin 1982; Dresp et al. 2005; Jouventin et al. 2005; Nolan et al. 2006; McGraw et al. 2007; Dobson et al. 2008; Jouventin et al. 2008; Pincemy et al. 2009) in which (i) both sexes invest about 14 months in egg and chick care to successfully fledge their single offspring (Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996), (ii) a male-biased sex-ratio in the pairing population has been reported (Pincemy et al. 2009, 2010), and both sexes appear to be choosy (Nolan et al. 2010). Results of mate choice experiments show that for some ornaments males experience a stronger intersexual selection than females (Pincemy et al. 2009; Dobson et al. 2011), suggesting that we might also expect a stronger male than female involvement in same-sex contests over mates. We tested this hypothesis by determining the frequencies of male and female involvement in trio parades.

King penguin trio parades were observed by Jouventin (1982) and studied in the congeneric emperor penguin *Aptenodytes forsteri* (Prévost 1961; Mougin 1966; Isenmann 1971; Jouventin et al. 1979). In both species, trio parades are frequent at the beginning of the pair formation season, and form when a solitary individual joins a pair, perhaps after being attracted by the vocalizations of the pair. Trio formations exhibit a typical pattern, where one individual leads the parade while the two others follow it and fight each other (I. Keddar & F.S. Dobson, pers. obs.). In the king penguin, the higher choosiness of females for male colour ornaments suggested that we should observe more trio parades involving male-male fights, and fewer trio parades involving female-female fights, than expected under the null hypothesis of equal investment in mate competition between the sexes. Thus, we specifically predicted that significantly more trios would exhibit pairs of combative males, that “joining”

individuals would most often be males, and that a single female would most often lead these trios.

A second aim of our study was to investigate the existence of within-sex differences in colour ornaments between individuals involved in such trios and individuals already paired, in order to know if competing birds are equal in their traits to those that have already been chosen as partners.

2.2. Methods

The king penguin is a long-lived pelagic seabird that breeds throughout the sub Antarctic islands from October to March (Stonehouse 1960). Our study took place at Cap Ratmanoff (-49°12'N, 70°33'E), Kerguelen Island, where we worked in a colony of approximately 80,000 pairs in January 2011. Three observers searched for trio parades in the colony. When a parade was spotted, the observers recorded the position of each individual, which allowed the identification of the leader and the two followers. As soon as an agonistic interaction between the followers of the parade was seen, each observer was assigned an individual for hand capture. A hood was placed over each bird's head immediately after capture, and kept throughout the handling period (less than 15 minutes), so that birds stayed calm. One hundred microliters of blood was drawn from of a brachial vein of each individual and preserved in Queen's buffer for later molecular sexing (Fridolfsson & Ellegren 1999). Twenty trios were studied; to avoid catching the same individual twice, each was color-marked with porcimark colored dye (Kruuse, Langeskov, Denmark) and then released.

We measured colour ornaments (auricular and beak) of 9 trios (9 females and 18 males). We used a USB2000 spectrophotometer and a PX2 pulsed-xenon light, calibrated against a WS-1 white standard (Ocean Optics Inc., Dunedin, FL, U.S.A.). Measurements were taken with the probe held perpendicularly to the ornaments, which yielded a reflectance spectrum ranging from 300 to 700 nm. In order to increase the accuracy of colour measurements, each ornament was measured three times (Falconer & Mackay 1996, p. 139-141) and spectra were averaged using Avicol 6.0 (Gomez 2006). These multiple measurements were necessary, given the overall moderate repeatability of our color measures (median = 0.5; 1st quartile = 0.4; 3rd quartile = 0.6; range: [0.3 : 0.9]). Computing tristimulus colour variables (i.e. hue, saturation, and brightness) summarized spectral data. Due to the bimodal distribution of beak spot colour reflectance, however, we split the spectrum of this ornament in half and defined an ultraviolet-blue (UV-blue) part between 300 and 499 nm

(with peak reflectance usually below 400 nm, thus in the near ultraviolet), and an orange part between 500 and 700 nm (Fig.1). Hue, saturation and brightness of the auricular patch were calculated after formulae H_3, S_8 and B_2 from Hill & McGraw (2006, p.108), respectively. Briefly, auricular hue was calculated as the wavelength at which the reflectance was halfway between its maximum and its minimum; auricular saturation (i.e. spectral purity of the ornament) was calculated as the difference between maximum and minimum reflectance across the whole spectrum, divided by the mean brightness of the spectrum; mean brightness was calculated as the sum of the reflectance values at each nm between 300 and 700 nm, divided by the number of values added across the whole spectrum (*i.e.* 401). UV-blue saturation and mean brightness of the beak spot, as well as orange hue, saturation and mean brightness, were calculated following the same principle except that the range of computation was restricted to 300-499 nm for the UV-blue, and to 500-700 nm for the orange. Finally, UV-blue hue was calculated as the wavelength of maximum reflectance between 300 and 499 nm.

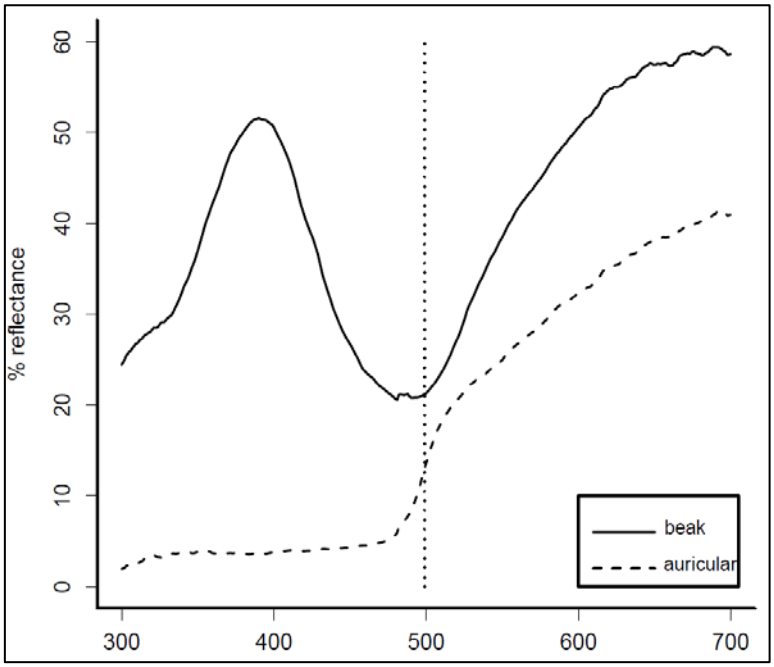

Figure 1. Example of reflectance spectra of the beak spot (solid line) and of the auricular patch (dashed line). The vertical dotted line shows the separation between the bell-shaped ultraviolet-blue reflecting part of the beak spot (300 to 499 nm) and the orange reflecting part of the beak spot (500-700 nm).

Statistical analyses

All statistical analyses were performed using R v2.15 (R development team 2012). We used the ratio of displaying males to females (*i.e.* adult individuals ready to mate) as an estimate of the colony OSR. We first tested whether the sex composition of the trio parades reflected the OSR (*i.e.* if they were randomly formed with respect to sex), or if it reflected a higher involvement from the males. Previous studies in our colony reported a sex ratio of displaying adults that ranged between 1.67 (Pincemy et al. 2010) and 1.96 (Pincemy et al. 2009). Given our hypothesis of stronger mate competition in males, we conservatively used the latter male-biased sex-ratio in our calculations of the expected frequencies of the sexes in trio parades. Under the null hypothesis of random trio parade formation, we considered a trio as the result of a Bernoulli trial repeated 3 times, with $p = 0.66$ the probability of randomly sampling a male, and $(1-p) = 0.34$ the probability of randomly sampling a female. The expected frequencies of each combination were compared to the observed values with a χ^2 goodness of fit test. Because one of the expected counts was less than 5, we computed the χ^2 statistics using a simulation estimate of the exact test probability based on a binomial distribution and 10 000 replicates (Sokal & Rohlf 1995, p. 702).

We then examined the chance that a pair was joined by a male individual, assuming that previously formed pairs were usually a male and a female, unless a unisex trio occurred (Pincemy et al. 2010). For this analysis, the frequency of putative "joiners" to form trios was compared to the estimated sex ratio of displaying males in the colony, using a binomial test. Finally, for the parades that included a single female, we tested if the female led trios more often than expected by chance, using a χ^2 goodness of fit test. If a female could occupy positions 1, 2, or 3 in a parade, then the probability that she would lead is $1/3$ at random.

We finally compared the colour differences between paired males and females from the colony at large with individuals involved in trios, using non-parametric tests due to non-normality (Mann-Whitney U test, Sokal & Rohlf 1995, p. 427). As we were mainly interested in differences between individuals in pairs and individuals involved in trios, we treated males and females separately. For each sex, we compared hue, saturation and mean brightness of the auricular patch, and of the UV-blue and orange colours of the beak spot. We applied Bonferroni corrections in order to take into account these multiple testings (9 tests for each sex), and lowered the significance threshold to 0.006 (Sokal & Rohlf 1995, p. 240).

2.3. Results

Among the 20 trios captured, 19 (95%) were composed of one female with two males; one (5%) was an association of 3 males. These observed frequencies differ significantly from those expected under the hypothesis of a random formation of the trio parades (χ^2=20.79, N=20, d.f.=3, P=0.0017; Table 1). If we assume that a trio parade forms when a solitary individual joins a pair (Jouventin 1982), they should originate from 19 male-female pairs and 1 male-male pair, all joined by a solitary male. Examination of the binomial distribution B(20,0.66) shows that the probability of observing this result at random is very low (P = 0.0002); thus the bias toward males in trio parades does not simply result from the existing male-biased sex ratio in the colony. Finally, females led all of the 19 mixed sex parades (100% versus 33% expected; χ^2 = 38.00, N = 19, d.f. = 2, P < 0.0001).

Table 1. Expected and observed frequencies of the possible trio parade combinations. Expected frequencies are for a population with 66% males and 34% females. M=male; F=female. The sample contained 20 trios. Expected and observed distributions were significantly different (see text).

	frequencies	
trio parade	expected	observed
MMM	0.29	0.05
MMF	0.44	0.95
MFF	0.23	0
FFF	0.04	0

The difference between UV-blue hue of beak spot of males in pairs and males in trios was significant before Bonferroni corrections (U = 825.5, P = 0.017, N_1 = 67, N_2 = 18), with males in trios more UV than paired males. After Bonferroni corrections, however, no statistically significant differences were found between colour ornaments of previously paired individuals and colour ornaments of individuals involved in trios for both sexes and all three tristimulus variables (Mann-Whitney tests; all U≤ 825.5, P > 0.01, N_1 = 67, N_2 = 18, for males; all U < 401, P > 0.1, N_1 = 67, N_2 = 9, for females). Small sample size of individuals involved in trios hinder the detection of statistically significant differences; an *a posteriori* power analysis showed that no significant differences could be detected below 32 trio individuals (80% power, 0.05% significance; Champely 2012). However, in spite of the small

statistical power of our analysis, a closer inspection of the results reveal an interesting difference which might have a biological relevance: males involved in trio parades had the median UV-blue hue of their beak spot 8 nm lower (viz., more in the ultraviolet) than males already paired (Table 2; see discussion). If we average the colour measures of males involved in a same trio in order to control for their non-statistical independence, the difference in UV-blue hue remains almost unchanged (median and 95% C.I. of UV hue if not averaged: 373 nm [370:382], see table 2; median and 95% C.I. of UV hue if averaged: 375 nm [371:378]).

Table 2. Within-sex differences in median hue, saturation and brightness between paired individuals and individuals involved in trios. Between brackets: 95% confidence intervals. In bold: significant difference without Bonferroni correction.

		Hue		Saturation		Mean Brightness	
auricular patch - yellow	paired males	526	[517 : 536]	2.0	[1.8 : 2.2]	11.5	[09.5 : 13.4]
	trio males	525	[516 : 530]	1.9	[1.7 : 2.1]	12.0	[10.0 : 13.4]
	paired females	522	[514 : 531]	2.0	[1.8 : 2.1]	12.2	[10.2 : 14.6]
	trio females	515	[514 : 526]	1.8	[1.6 : 2.0]	12.4	[11.3 : 15.1]
beak spot - orange	paired males	556	[553 : 560]	0.64	[0.60 : 0.69]	52.3	[46.1 : 57.7]
	trio males	557	[554 : 558]	0.61	[0.59 : 0.67]	50.3	[41.1 : 54.2]
	paired females	558	[555 : 560]	0.60	[0.57 : 0.64]	56.4	[49.2 : 60.1]
	trio females	555	[554 : 556]	0.55	[0.54 : 0.66]	47.6	[44.8 : 50.0]
beak spot - UV-blue	paired males	**381**	**[377 : 386]**	0.75	[0.67 : 0.84]	42.4	[35.4 : 48.2]
	trio males	**373**	**[370 : 382]**	0.7	[0.65 : 0.87]	42.7	[32.9 : 47.4]
	paired females	386	[380 : 391]	0.66	[0.61 : 0.74]	45.7	[39.4 : 51.1]
	trio females	384	[373 : 387]	0.66	[0.55 : 0.89]	42.3	[34.2 : 44.8]

2.4. Discussion

Between-sex differences in intrasexual selection

The first aim of our study was to compare the relative strength of intrasexual selection in males and females king penguins, by determining the sex-composition of trio parades. We found that as predicted this selection was highly biased toward males, with 19 out of 20 trio parades formed by two males fighting over a female; the 20th parade was formed by three males. It is likely that males joined pairs, thus initiating trio parades in all 20 cases. And finally, females led trios in all 19 cases in which a female occurred. Thus, all lines of evidence supported the hypothesis that males competed for females mates more strongly than females competed for males. These tests support our initial suspicion for this hypothesis, based on the sex ratio of displaying king penguins (and our best estimate of the OSR) and previous comparative and experimental evidence (Pincemy et al. 2009; Nolan 2010; Dobson et al. 2011), that males likely compete very strongly for mates. Thus, intrasexual selection in a king penguins colony where OSR is male-biased follows the typical pattern of mate competition observed in species in which sexual dimorphisms and OSR are male-biased (Weir et al. 2011). The generality of this result in other mutually ornamented species (reviewed in Kraaijeveld et al. 2007) would require further investigation.

A recent review reports that female-female contests over mates are frequent across animal taxa, thought the competition was based primarily on quality (e.g. direct benefits through paternal care) rather than quantity of mates (Rosvall 2011). It is thus surprising that we did not observe any trio involving two females in a species for which extensive biparental care is of crucial importance for offspring survival, and where paternal care is slightly higher than maternal care (Stonehouse 1960; le Bohec et al. 2007; Saraux et al. 2012). In the king penguin, however, same-sex agonistic interactions do not always lead to the formation of a trio parade: an unmated individual approaching a pair can quickly leave after being pecked at by the partner of the same sex (Jouventin 1982; I. Keddar & F.S. Dobson, pers. obs.). The relative involvement of each sex in such interactions is not documented, leaving open the possibility that intrasexual selection exists in females too; however, even if female-female aggressive behaviour exists, our present results suggest that males have a much greater propensity than females to escalate the conflict up to the formation of a trio parade, the most intense form of intrasexual selection in this species.

We also reported one trio parade formed by three males. Unisex trio parades may be the result of highly motivated individuals and/or inexperienced breeders seeking to pair.

Indeed, male-male homosexual mating displays have been observed in about a quarter of displaying pairs in our king penguin colony, and the males involved in such displays take longer to pair with a female than heterosexual displaying males (Pincemy et al. 2010).

In king penguins, a pair produces a single egg at each breeding attempt and both sexes invest about 14 months in egg and chick care (Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996). Hence, under a male biased OSR the number of breeding males for a given reproductive season will be limited by the total number of breeding females, which suggests a strong positive relationship between the OSR and the intensity of male-male competition. Interestingly, however, Stonehouse (1960) observed that males tend to invest more than females in chick feeding before fledging; or differently said, when year *t+1* begins (viz., at month 12 of the 14-months egg and chick developmental period), successful breeding males have a higher propensity to invest in paternal care until fledging than to desert and start a new breeding cycle right away. In addition, males always take the first standing shift with the egg at the beginning of breeding (Weimerskirch et al. 1992; Olsson 1996). Greater paternal investment under strong mating competition has been theoretically predicted (Kokko & Jennions 2008) and is empirically supported (reviewed in Weir et al. 2011), but the king penguin is, to our knowledge, the first species exhibiting both male-biased contests over mates and male-biased parental care. This finding is puzzling, and because the origin of the male-biased OSR is unknown, hard to interpret. Besides understanding the origin of the male biased OSR, it may prove fruitful to study (i) OSR fluctuations over the period of successful breeding, and (ii) how males trade-off their investment in care between the fledging period and the next breeding attempt.

The male-biased investment in same-sex contests over mates might be one of the selection pressures (though not necessary the only one) explaining male-biased sexual dimorphisms in body size (Pincemy et al. 2009) and auricular patch size (Dobson et al. 2011). Indeed, large body size in males is often selected by aggressive male contests (reviewed in Andersson 1994, p. 132). A previous study reported a correlation between auricular patch size and aggressiveness in both sexes while individuals were defending their breeding territory and single egg within the colony (Viera et al. 2008). If one or both of these traits have a heritable basis and their degree of development gives their bearer an advantage in access to mates, some degree of sexual dimorphism in body size or auricular patch size should evolve. Future work might investigate in more details the characteristics of males involved in such parades, as well as the characteristics of the loser and the winner of the fight. We predict that heavier

individuals and those expressing the larger ear patches should have a higher probability of winning fights.

Within-sex colour differences

The second aim of our study was to test the existence of within-sex differences between colour ornaments of individuals involved in trio parades and individuals already paired. Although statistically insignificant, comparison of colour ornaments revealed that the UV-blue hue of the beak spot was about 8 nm lower (viz., more in the ultraviolet) for males in trios than for paired males. Actually, however, we have little information to convincingly explain this difference, and further investigations are necessary. A promising avenue would be the fine observation of how conflicts escalate up to the formation of a trio parade (see above), as it may help to understand if, for example, some males have greater propensity than others to escalate a conflict, or if females involved in trios are more sought-after mates than other females.

Nonetheless, we are confident that the differences in UV-blue hue of male beak spots highlighted in our study can be perceived by the birds. The recent sequencing of SWS1 opsin revealed that king penguin eyes possess violet-sensitive cones (Capuska et al. 2011) with a theoretical maximum peak sensitivity at 405 nm (Ödeen & Håstad 2003). Although the peak of the UV-blue signal of the beak spot (Table 2) and the theoretical maximum peak sensitivity of the violet-sensitive cones are not perfectly matched, most of the UV-blue signal variation should be perceived, as suggested by avian vision characteristics (see fig.1 in Endler & Mielke 2005) and by experimental manipulation of UV-blue beak colour in king penguins (Nolan et al. 2010).

Interestingly, the reflectance spectrum of the beak spot presents a structural UV-blue reflecting part (Dresp et al. 2005; Dresp & Langley 2006) and a carotenoid-based orange reflecting part (unpublished results cited in McGraw et al. 2007); whether the UV-blue signal of the beak spot is perceived as a separate colour or is contributing to amplify the orange signal (Shawkey & Hill 2005) is unknown, and answering this question would require testing the king penguins' colour perception.

Conclusion

Our results show that the relative involvement of each sex in king penguins trio parades is strongly biased toward males. We cannot exclude that females may compete over mates in other contexts; however, trio parades are the most intense form of intrasexual selection in this species, and we conclude that OSR and intrasexual selection are strongly biased toward males in our colony. This conclusion supports the classical predictions of the effect of OSR on the intensity of intrasexual selection; to the best of our knowledge, however, king penguins are a species in which the sexes express very similar colour ornaments. Finally, the beak spot of males in trios reflect more in the ultraviolet than the beak spot of males in pairs (although due to small sample size the difference was not statistically significant). Actual knowledge of king penguins' visual system suggests that females should perceive this difference, but understanding its biological meaning would require further investigations.

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3. Mutual mate choice in the king penguin: selection of ultraviolet color of the beak spot, and homogamy within definitive pairs

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Sexual selection explains sexual dimorphism in ornaments used in mate choice, but has more difficulty explaining monomorphic sexual ornaments. Mutual mate choice is a form of sexual selection that might explain such monomorphism. We tested the mutual mate choice hypothesis in a mutually ornamented seabird, the King penguin *Aptenodytes patagonicus*, through observations of the pair formation process in the field. Penguins that are ready to mate form displaying pairs during the breeding season. Some of these pairs become definitive and produce an egg, while other pairs separate and switch to another potential partner (temporary pairs). We compared color ornaments (UV and orange beak spot, yellow auricular patch, and brown to bright yellow gradient on the breast) of individuals in definitive and temporary pairs. We found homogamy for UV color of the beak spot between members of definitive pairs, but not between members of temporary pairs. Moreover, females involved in definitive pairs expressed a more UV hued beak spot than females involved in temporary pairs. This latter result may reflect male choice of mates, surprising since all previous studies found that males were under stronger sexual selection than females. The mutual mate choice hypothesis was supported for UV color of the beak spot, but not for color or size of the auricular patch of feathers, nor for the feather color of the breast patch.

Keywords: sexual selection, mutual mate choice hypothesis, mutual ornamentation, seabird, *Aptenodytes patagonicus*

3.1. Introduction

Sexual selection theory aims to explain the evolution and maintenance of secondary sexual traits (Darwin 1871). Such traits can be behavioral (e.g. male song in European starlings, *Sturnus vilgaris*: Eens et al. 1991), morphological (e.g. antlers of male red deer, *Cervus elaphus*: Clutton-Brock et al. 1982), or biochemical (e.g. cuticular hydrocarbons in fruit flies, *Drosophila serrata*: Chenoweth & Blows 2005), and are used to gain advantages in the competition among same-sex individuals for access to opposite-sex partners and their gametes. The process of sexual selection can operate through two modalities: intrasexual competition and intersexual mate choice. The former encompasses all situations involving interactions between individuals of the same sex (e.g. male fights in elephant seals, *Mirounga sp*.: Hoelzel et al. 1999), while the latter is an indirect competition between same-sex individuals arbitrated by the mate choice of members of the opposite-sex (e.g. female mate choice in long-tailed widowbirds, *Euplectes progne*: Andersson 1982).

Among the diversity of forms that secondary sexual traits can take on, ornamental colors are among the most studied, especially in birds (Hill 2006). Sexually dimorphic species have received a lot of attention, and the common pattern where males are ornamented and females choosy is explained by sex differences in parental investment (Trivers 1972; Kokko & Johnstone 2002). Under this scenario, females face more mating opportunities than they can realize, and should exhibit some discrimination among potential partners in order to choose those that produce the most or best offspring. To the contrary, males face a limited number of mating opportunities, and should express traits such as colored ornaments that increase the chance of mating with multiple partners. Color ornaments often convey important information about their bearer, such as age, strength of the immune system, or parental ability (reviewed in Hill & McGraw 2006). These ornaments thus play an important role in the process of mate choice (Darwin 1871; Andersson 1994).

In some species, however, ornamental colors are expressed in both males and females (Kraaijeveld et al. 2007). Two hypothesis have been proposed to explain the expression of such conspicuous ornaments in both sexes: (i) the genetic correlation hypothesis (Lande 1980), according to which color ornaments are functional in one sex (usually males) and non-functional in the other (usually females), and (ii) the mutual selection hypothesis, according to which elaborate characters are the result of a selection for their expression in both sexes. Under this last scenario, such ornaments should result from competition over sexual and/or non-sexual resources (the social selection hypothesis; West-Eberhard 1979, 1983). Mutual

competition for sexual resources (the mutual mate choice hypothesis; Huxley 1914) is expected in species exhibiting high and similar investment by both sexes in raising offspring (Kokko & Johnstone 2002). Recently the maintenance of mutual color ornaments received increased interest in seabirds (e.g. Least auklet *Aethia pusilla*: Jones & Montgomerie 1992; Crested auklet *Aethia cristatella*: Jones & Hunter 1993; Great cormorant *Phalacrocorax carbo*: Childress & Bennun 2002; Yellow-eyed penguin *Megadyptes antipodes*: Massaro et al. 2003), and more particularly in the king penguin *Aptenodytes patagonicus.*

Adult king penguins of both sexes exhibit two yellow auricular patches of feathers, a patch of feathers on the breast that grades from brown at the throat to bright yellow on the breast, and an orange and ultraviolet spot on each side of the lower mandible (Jouventin 1982; Dresp et al. 2005; Jouventin et al. 2005; Dresp & Langley 2006; Nolan et al. 2006, 2010; McGraw et al. 2007; Dobson et al. 2008; Jouventin et al. 2008; Pincemy et al. 2009; Dobson et al. 2011). Moreover, both sexes invest 14-16 months in parental care to successfully fledge their single offspring (Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996). These characteristics suggest that mutual mate choice may occur in the king penguin (Kokko & Johnstone 2002).

In a recent observational study, Dobson et al. (2008) found that king penguins breeding early in the season (i.e. starting courtship between mid-November and early December: Stonehouse 1960; Olsson 1996) paired assortatively according to ultraviolet and orange colors of their beak spot, and this was not the case for late breeders (i.e. stating courtship in mid-January: Stonehouse 1960; Olsson 1996). These results suggested that among early breeders ultraviolet and orange colors of the beak spot were of importance in both sexes. In subsequent experimental work, alteration of ultraviolet reflectance of the beak spots delayed pairing in both sexes (Nolan et al. 2010), alteration of auricular and breast color feathers delayed pairing in males (Pincemy et al. 2009), and reduction of the size of the auricular patches delayed pairing in males (Pincemy et al. 2009; Nolan et al. 2010). However, some modifications of the color ornaments may have altered their appearance beyond their natural range of variation (Pincemy et al. 2009; Nolan et al. 2010), and might have stimulated unusual responses from pairing individuals. In the present work, we tested the mutual mate choice hypothesis through direct observations of the pairing process among unmodified early breeders.

The king penguins' breeding season begins in the austral spring, when birds come ashore and form dense colonies throughout the sub-Antarctic islands (Williams 1995; Olsson 1996). Individuals that are ready to mate display to potential partners around the fringes of the

colony, forming temporary pairs. Eventually, some of these pairs become definitive and produce an egg; while in others pairs, partners separate and perhaps switch to a new potential partner (Olsson 2001). We surmised that if members of a temporary pair separated, one (or both) of them was perceived as unattractive, whereas if a temporary pair became a definitive one, each of its members was perceived as suitable for producing an egg and raising a chick. We tested the mutual mate choice hypothesis through three predictions. First, we should observe a stronger degree of assortment between color ornaments of members of definitive pairs than between color ornaments of members of temporary pairs. Second, members of definitive pairs should express stronger color ornaments than members of temporary pairs. Although both sexes express color signals of the roughly same magnitude, one sex could be choosier, subjecting the other sex to a stronger selection pressure (Kokko & Johnstone 2002); thus, males and females were tested separately. Third, if color ornaments reflect body condition, we should observe a positive association between aspects of the ornaments and either body mass or a derived condition index. This last prediction is drawn from the reasonable expectation that ornaments depend on body condition (Zahavi 1975) and that they honestly reflect the general well being of individuals (Kodric-Brown & Brown 1984). We tested these predictions by measuring body mass, body size, and the color and size of ornaments of displaying pairs, and following these pairs until their separation or the laying of an egg.

3.2. Methods

Study area and data collection

We studied king penguins in a breeding colony (approximately 80 000 pairs) at Cap Ratmanoff (49°12’S, 70°33’E), Kerguelen Islands, from November 2008 to January 2009. Captures were made from 23 November to 12 December. Before capturing a displaying pair, we ensured that both members had learnt each other’s call -an essential part of the pairing process (Jouventin 1972)- and would thus easily reunite if separated (e.g., subsequent to release after being measured). This was accomplished by walking between displaying pairs, so that visual contact between the pair was lost, and then observing them reunite by calling and walking back into close association. We captured both members of 73 displaying pairs. A hood was placed over each bird’s head immediately after capture, and kept throughout the handling period (about 20 minutes for each pair), so that birds stayed calm.

Individuals were weighted to the nearest 0.1 kg with and electronic balance, and flipper length was measured to the nearest mm. We used the residuals of the ordinary least square regression of body mass on flipper length as an index of body condition. Auricular patch width and the distance between the two auricular patches were measured with a caliper to the nearest 0.1 mm. One hundred microliters of blood was drawn from of a brachial vein of each individual and preserved in Queen's buffer for later molecular sexing (Fridolfsson and Ellegren 1999). We measured color of the beak spot, and of the auricular and breast patches ("feather ornaments") of 146 individuals. We used a USB2000 spectrophotometer and a PX2 pulsed-xenon light, calibrated against a WS-1 white standard (Ocean Optics Inc., Dunedin, FL, U.S.A.). Measurements were taken with the probe held perpendicularly to the ornaments, which yielded a reflectance spectrum ranging from 300 to 700 nm. Each ornament was measured three times and spectra were averaged using Avicol 6.0 (Gomez 2006).

Each bird was temporary marked with a numbered plastic band placed around each flipper, and these numbers were subsequently easily visible using binoculars during surveys of the colony. Censuses of all marked penguins, including identity, behavior, location, and presence of a partner, were recorded twice each day, at about 6:00 and 18:00. After handling, the two members of a pair were released at the point of capture. Bands were removed after the field study.

Color analyses

Tristimulus color variables (i.e. hue, saturation, and brightness) were calculated to summarize spectral data (Montgomerie 2006). Hue corresponds to what is commonly called "color". It indicates which wavelengths contribute the most to the color signal emitted from an ornament expressed by a sender, and partly determines the degree of activation of each cone type in the retina of a receiver (i.e. the perceived signal). Saturation is a measure of spectral purity, indicating the degree to which a color appears as composed of single wavelength. This measure has been related to the pigment content of ornaments in a few species (e.g. Snares penguins *Eudyptes robustus* yellow feathers: McGraw et al. 2009; mallard *Anas platyrhynchos* beaks: Butler et al. 2011). Brightness is a measure of spectral intensity, indicating the total amount of light coming from an ornament.

Hue, saturation and brightness of the feather ornaments were calculated after formulae H_3, S_8 and B_2 from Montgomerie (2006, p.108), respectively. Briefly, hue was calculated as the wavelength at which the reflectance was halfway between its maximum and minimum values. Saturation was calculated as the difference between maximum and minimum

reflectance across the whole spectrum, divided by the mean brightness of the spectrum. Mean brightness was calculated as the sum of the reflectance values between 300 and 700 nm, divided by the number of values (viz., sampling points) across the whole spectrum. Due to the bimodal distribution of beak spot color reflectance, we split the spectrum of this ornament in half and defined an ultraviolet (UV) part between 300 and 499 nm (with peak reflectance usually below 400 nm), and a yellow-orange part between 500 and 700 nm (figure 1). UV saturation and mean brightness, as well as yellow-orange hue, saturation and mean brightness of the beak spot were calculated following the same principles described above, except that the range of computation was restricted to 300-499 nm for the UV, and to 500-700 nm for the yellow-orange. Finally, UV hue of the beak spot was calculated as the wavelength at maximum reflectance between 300 and 499 nm.

Color spectra exhibited two kinds of shapes: UV color was bell-shaped, while other colors were S-shaped (figure 1). For each color, saturation and brightness are physically linked. Indeed, saturation is a measure of spectral purity: the higher the saturation of a color the narrower the range of reflected wavelengths, thus the lower the brightness. And, reciprocally, the lower the saturation the broader the range of reflected wavelengths, thus the higher the brightness.

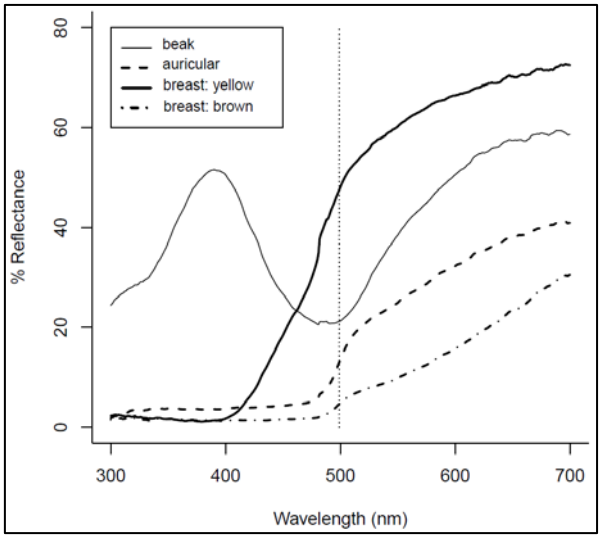

Figure 1. Example of reflectance spectra of the beak spot, auricular patch, brown part of the breast patch, and yellow part of the breast patch. The vertical dotted line show the separation between the bell-shaped UV reflecting part of the beak spot (300-499 nm) and the orange reflecting part of the beak spot (500-700 nm).

Statistical analyses

All statistical analyses were performed using R 2.15.2 (R core team 2012). Sexual dimorphisms in body mass and body size were tested using t-tests. An extended analysis of sexual dimorphism has been published using the same dataset in a preceding study (Dobson et al. 2011). Differences in body mass and body condition between males or females that stayed with or separated from their initial partner were tested with two-way analyses of variance.

Relationships between the tristimulus color variables of each ornament were studied with Pearson correlation coefficients. Due to the multiple tests performed, Bonferroni corrections were applied. The significance level was lowered to 0.05/3 = 0.017 for feather ornaments. Moreover, tristimulus variables of UV and orange of the beak spot were all tested against each other, and the significance level was therefore lowered to 0.05/15 = 0.003. These tests revealed some degree of collinearity (see results); we chose, however, to not regroup these tristimulus variables into single color scores because they have their own biological interpretations (see above). Relationships between pair members were also studied with Pearson correlation coefficients. Twenty traits were tested (15 color traits plus body mass, body size, body condition index, auricular width, and inter-auricular distance); therefore, the significance threshold was lowered to 0.05/20 = 0.0025. When necessary, these Pearson correlation coefficients were compared using Fisher's z transformation. Finally, the relationships between ornaments (15 color variables plus auricular width and inter-auricular distance) and body mass, body condition, and flipper length were also tests with Pearson correlation coefficients, with a significance threshold lowered to 0.05/17 = 0.003.

The influence of the morphometric and color traits (20 traits studied) on the pairing status of sampled individuals (i.e., if they stayed with or separated from their initial partner) was assessed with binomial generalized linear models, through a double approach combining model selection based on the lowest Akaike Information Criterion corrected for small sample size (AICc; Hurvich & Tsai 1989; Burnham & Anderson 2002) and stepwise regressions. Model selection was performed using the automated procedure provided by the R package glmulti 1.0.6 (Calcagno & de Mazancourt 2010). A recent analysis showed that model selection was unaffected by moderate levels of collinearity (Freckleton 2011); however, some of the traits measured showed high levels of collinearity (Pearson correlation coefficient >0.5; see results). To alleviate this problem, we proceeded in two steps. First, an *initial set* of full models was built. Each model within this initial set was a unique combination of variables with low to moderate collinearity. Due to the complex patterns of correlations, this initial set included 72 (exhaustive) unique combinations. Second, the automated selection procedure

was run for each of the 72 models from the initial set. Each run of the procedure returned a *confidence set* of 100 models, and the relative frequency of each trait within a confidence set was used as an index of its importance (e.g. 0.5 for a trait retained in half of the model within a confidence set). The respective indexes of importance computed for each trait after the 72 runs were then averaged to estimate their overall importance on the pairing process.

Ethical note

Animal handling and measurements carried out in this study comply with current French laws and were approved by the Ethical Committee of the French Polar Institute (IPEV Program ETHOTAAF No. 354).

3.3. Results

Body condition

Overall, males were 11.9 % heavier than females (males, mean ± s.e. = 12.2 kg ± 0.1; females, mean ± s.e. = 10.9 kg ± 0.1; t = 8.72, df = 144, P < 0.0001) and 3.2 % longer in flipper length (males, mean ± s.e. = 322 mm ± 1.1; females, mean ± s.e. = 312 mm ± 1.3; t = 5.81, df = 144, P < 0.0001). Thus, parameters of the ordinary least square regression of body size on flipper length were estimated separately for each sex. Body mass was significantly associated with flipper length in both sexes (males: R^2 = 0.14, F = 11.81, df = 1,71, P = 0.0001; females: R^2 = 0.22, F = 20.25, df = 1,71, P < 0.0001). The body condition index was not different between males and females nor between individuals that stayed with and individuals that separated from their initial partner (table 1), and no differences were observed between body mass of individuals that stayed together and body mass of individuals that separated (table 2).

Table 1 Effect of sex, status, and their interaction on body condition (two-way anova). s.d.: standard deviation; d.f.: degree of freedom

	Estimate ± s.d.	d.f.	t	P-value
Intercept	0.010 ± 0.13	71	0.074	0.94
Sex	0.098 ± 0.16	71	0.609	0.54
Status	-0.019 ± 0.18	71	-0.104	0.92
Sex : Status	-0.195 ± 0.23	71	-0.856	0.40

Table 2 Effect of sex, status, and their interaction on body mass (two-way anova). s.d.: standard deviation; d.f.: degree of freedom

	Estimate ± s.d.	d.f.	t	P-value
Intercept	10.83 ± 0.14	71	75.02	< 0.0001
Sex	1.47 ± 0.17	71	8.43	< 0.0001
Status	0.15 ± 0.20	71	0.73	0.47
Sex : Status	-0.43 ± 0.24	71	-1.74	0.09

Relationships between hue, saturation, and brightness of color ornaments

Auricular hue was strongly positively correlated with auricular saturation in the overall sample ($r = 0.91$, $df = 144$, $P < 0.0001$). Both hue and saturation of the auricular patch were highly negatively correlated with its brightness ($r = -0.77$ and $r = - 0.90$, respectively, both $df = 144$, $P < 0.0001$). Hue and saturation of the yellow part of the breast patch were highly correlated ($r = 0.75$, $df = 144$, $P < 0.0001$); hue and saturation were also negatively associated with brightness of the yellow part of the breast patch ($r = -0.55$ and $r =-0.84$, respectively, both $df = 144$, $P < 0.0001$). Hue, saturation, and brightness of the brown part of the breast were all significantly correlated (hue and saturation: $r = 0.70$; hue and brightness: $r = -0.76$; saturation and brightness: $r = -0.88$; $df = 144$, $P < 0.0001$ for each combination).

UV hue and saturation of the beak spot were negatively associated, but relatively weakly ($r = -0.33$, $df = 144$, $P < 0.0001$). Orange hue of the beak spot was not correlated to other measures (all $r < 0.17$, $df = 144$, $P > 0.07$). Finally, UV saturation, UV brightness, orange saturation, and orange brightness of the beak spot were all highly associated (UV saturation and UV brightness: $r = -0.69$; UV saturation and orange saturation: $r = 0.81$; UV saturation and orange brightness: $r = -0.73$; UV brightness and orange saturation: $r = -0.88$; UV brightness and orange brightness: $r = 0.97$; orange saturation and orange brightness: $r = -0.85$; $df = 144$, $P < 0.0001$ for each combination).

Assortment among pairs

For members of pairs that stayed together, a positive association was observed for UV saturation of the beak spot ($r = 0.55$, $df = 35$, $P = 0.0004$; figure 2). The associations between members of these pairs for UV brightness and orange brightness of the beak spot were not significant after Bonferroni corrections ($r = 0.35$, $df = 35$, $P = 0.03$ and $r = 0.38$, $df = 35$, $P = 0.02$, respectively). No other associations were observed between members of these definitive

pairs (all $r < 0.26$, all $df = 35$, all $P > 0.12$). Finally, no significant associations were observed between members of pairs that separated (all $r \leq 0.32$, all $df = 34$, all $P \geq 0.05$).

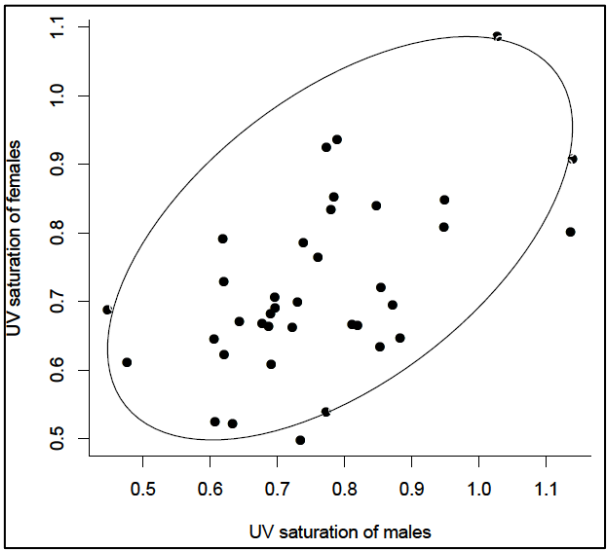

Figure 2. Correlation between UV saturation of the beak spot of mates that stayed together.

Variables influencing the pairing process

In females, AICc of the full models ranged from 109.7 to 107.7. The model selection procedure, based on the lowest AICc of competing models, identified two influential variables in the pairing process of females: the UV hue of the beak spot, which was retained every time (mean importance ± s.d. = 1.00 ± 0), and flipper length (mean importance ± s.d. = 0.84 ± 0.02). Other variables were retained less than half of the time (figure 3). AICc of the final model including only UV hue and flipper length was 98.07. The stepwise regression procedure, based on the deletion of non-significant effects, identified UV hue as significantly influencing the pairing process of females, and flipper length approached significance (table 3). Females that stayed with their initial partner displayed a beak spot more strongly UV in hue (mean ± s.e. = 382 nm ± 1.4; figure 4) and flippers slightly longer (mean ± s.e. = 315 mm ± 2.1) than females that separated from their initial partner (mean ± s.e. = 389 nm ± 1.7, and 310 mm ± 1.5, respectively).

Table 3 Factors influencing the pairing status of females, identified through the stepwise regression procedure applied to a generalized linear model. In bold: significant effect

	Estimate ± s.d.	z	P-value
Intercept	14.36 ± 11.90	1.21	0.228
UV hue	-0.07 ± 0.03	-2.69	**0.007**
flipper length	0.04 ±0.02	1.88	0.06

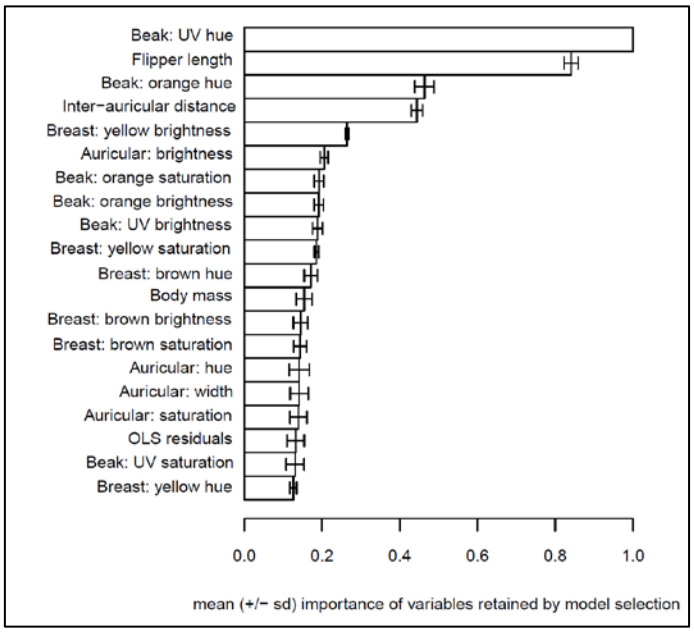

Figure 3. Mean importance (± s.d.) of variables in explaining the mating status of females. UV hue was retained in each model, and thus has a null standard deviation.

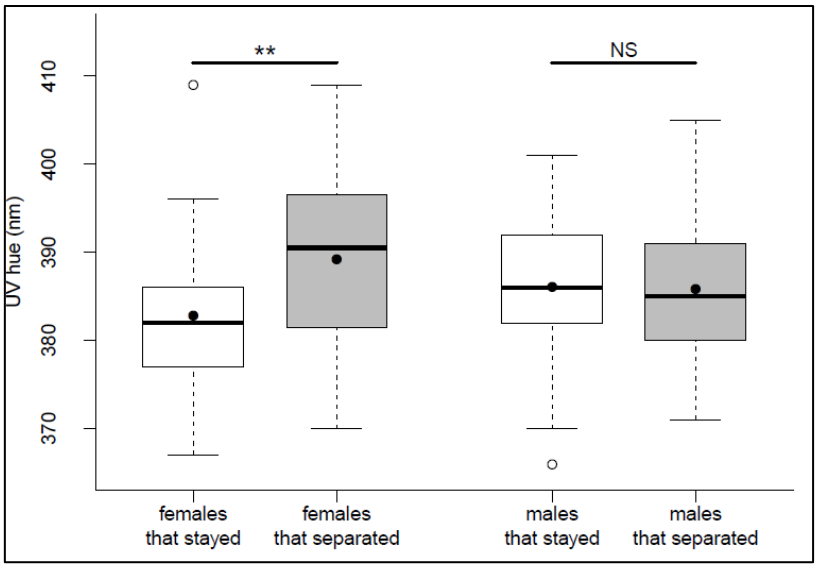

Figure 4. boxplots showing UV hue variation of the beak spot of males and females that stayed with their partner (white) and of males and females that that separated from their partner (grey). Horizontal bold lines: medians; black dots: means; top and bottom of the boxes: quartiles; bottom and top whiskers: respectively 0.05 and 0.95 quantiles; white dots: extreme data points; **: P-value = 0.007; NS: P-value not significant.

In males, AICc of the full models ranged from 119.2 to 116.3. None of the tested variables was found to influence their pairing process (figure 5). Male body mass, ranked as the most important one, was retained only half of the time by the model selection procedure (mean importance ± s.d. = 0.51 ± 0.02; figure 5). AICc of the model including male body mass and AICc of the void model were not very different (104.7 and 104.6, respectively). Auricular width, as well as UV hue, UV saturation, and UV brightness of the beak spot were ranked among the least important variables (mean importance ± s.d. of auricular width = 0.13 ± 0.02; mean importance ± s.d. of each of the UV color measures = 0.11 ± 0.01). The mean values of these variables in males that stayed and in males that separated were very close (table 4). Finally, none of the tested variables was found to have a significant effect on the male pairing process according to the stepwise regression procedure.

Table 4 Mean ± standard error of auricular width (mm), UV hue, UV saturation, and UV brightness of the beak spot of males that stayed with their initial partner and of males that separated from their initial partner

	males that stayed	males that separated
	mean ± s.e.	mean ± s.e.
auricular width	42.2 ± 0.6	42.2 ± 0.6
UV hue	386 ± 1.4	386 ± 1.3
UV saturation	0.76 ± 0.03	0.76 ± 0.03
UV brightness	46.5 ± 1.4	46.6 ± 1.7

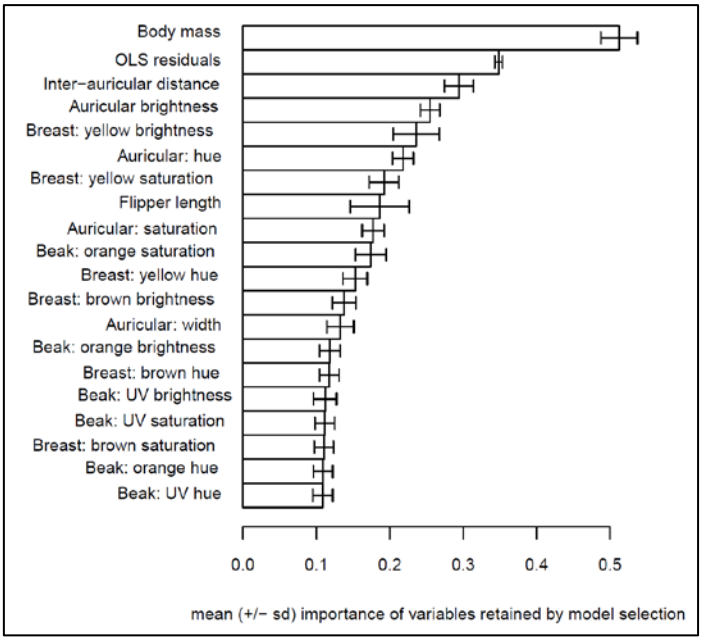

Figure 5. Mean importance (± s.d.) of variables in explaining the mating status of males.

Associations between ornaments and condition

Body mass and auricular width were positively correlated across the whole sample ($r = 0.42$, $df = 144$, $P < 0.0001$; figure 6). The same pattern of association was observed between the body condition index and auricular width, though the relation was weaker ($r = 0.29$, $df = 144$, $P < 0.0001$). In pairs that stayed together, flipper length was associated with UV saturation and UV brightness, although these relationships were not significant after threshold adjustment ($r = -0.26$, $df = 72$, $P = 0.03$, and $r = 0.37$, $df = 72$, $P < 0.0001$, respectively; figure

7). These correlations were similar in males and females (respectively: $r_1 = -0.26$, $r_2 = -0.39$, $z = -0.87$, $P = 0.38$; and $r_1 = 0.31$, $r_2 = 0.48$, $z = 1.21$, $P = 0.23$; all $n = 74$). Flipper length was also significantly associated with orange saturation and orange brightness of the beak spot ($r = -0.34$, $df = 72$, $P = 0.003$, and $r = 0.39$, $df = 72$, $P = 0.0007$, respectively; figure 8), and again these correlations were not different between the sexes (respectively: $r_1 = -0.40$, $r_2 = -0.41$, $z = -0.07$, $P = 0.94$; and $r_1 = 0.30$, $r_2 = 0.54$, $z = 1.76$, $P = 0.08$; all $n = 74$). Finally, these associations between flipper length and UV saturation, UV brightness, orange saturation or orange brightness were not observed in pairs that separated (all $r < 0.1$, all $df = 70$, all $P > 0.4$).

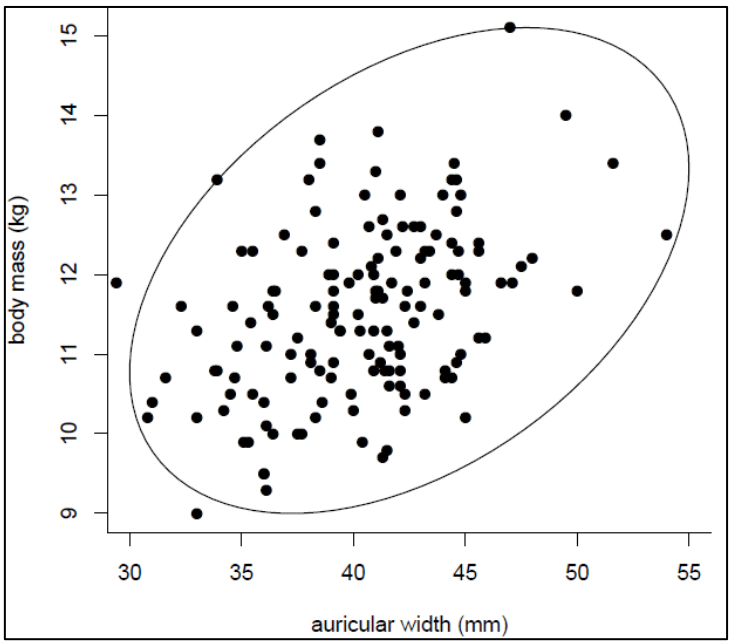

Figure 6. Correlation between body mass and auricular width of all sampled individuals.

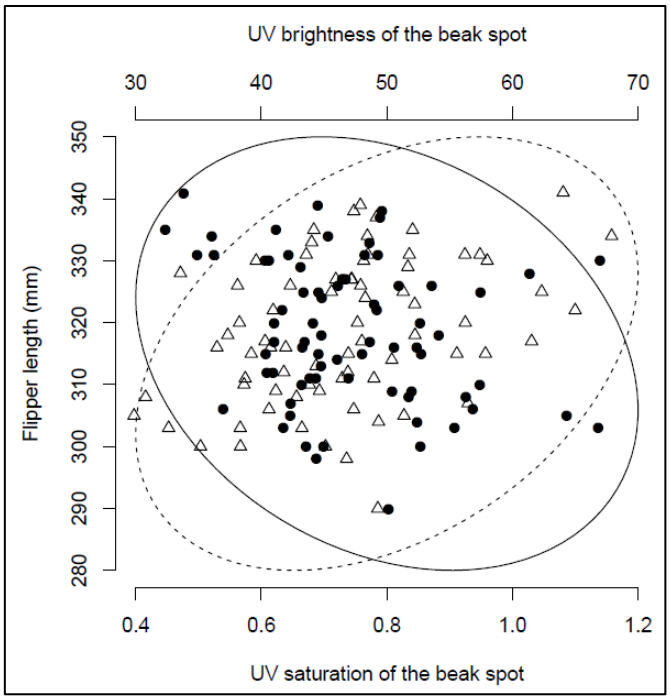

Figure 7. Correlation between flipper length and UV saturation of the beak spot (black dots and solid line), and between flipper length and UV brightness of the beak spot (white triangles and dashed lines), in individuals that stayed with their initial partner.

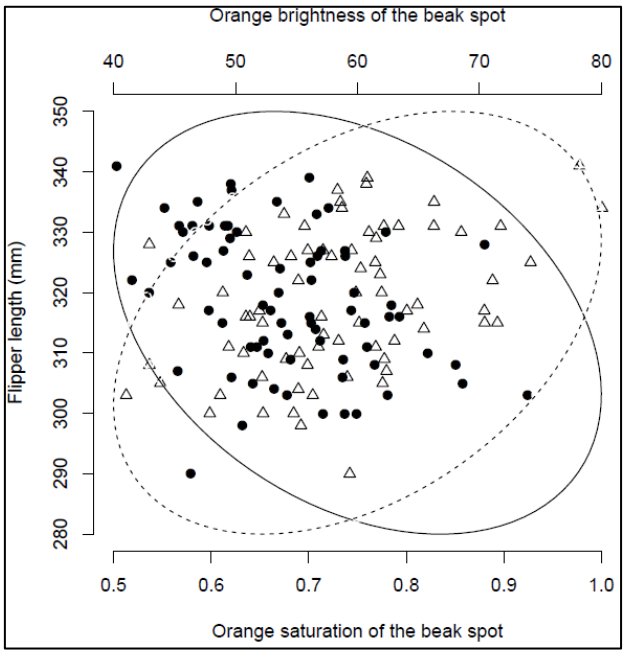

Figure 8. Correlation between flipper length and orange saturation of the beak spot (black dots and solid line), and between flipper length and orange brightness of the beak spot (white triangles and dashed lines), in individuals that stayed with their initial partner.

3.4. Discussion

Main results

We examined our results in tests of the hypothesis of mutual mate choice, using 3 primary predictions. First, that ornaments should reflect associative mating. This prediction was supported for UV saturation of the beak spot. A significant association was also observed for UV brightness and orange brightness of the beak spot before Bonferroni corrections. Second, that there should be a difference in the ornaments of members of pairs that split up before egg laying and members of pairs that initiated reproduction by egg laying and care. We observed that UV hue of the beak spot of females from definitive pairs was lower (*i.e.* shifted toward shorter wavelengths) than UV hue of the beak spot of females from pairs that separated; this difference, however, was not observed in males. Thus, the second prediction was only partly supported. Three, that there should be an association between ornaments and estimates of body size or condition. Auricular width significantly reflected body mass and condition among the overall sample of penguins. In addition, brighter beak spots were associated with larger individuals for definitive pairs, but not for failing ones. These results provide some support for both condition-dependence and the honest advertisement (of body size) hypothesis of mate choice.

Assortative mating within definitive pairs

Pairs that stayed together, but not pairs that separated, exhibited homogamy for UV saturation, UV brightness, and orange brightness of the beak spot. Moreover, UV saturation was associated to UV hue, and orange brightness was strongly associated to orange saturation of the beak spot. Therefore, with the exception of orange hue, all color measures of the beak spot showed positive associations within pairs that stayed together. As recently emphasized, however, the underlying mechanisms leading to homogamy remains in general largely unknown (Galipaud et al. 2013), and linking a mating pattern to a mating preference is challenging (Wagner 1998; Widemo & Sæther 1999). Nonetheless, previous experiments in which UV reflectance of the beak spot was altered produced delayed pairing in both sexes (Nolan et al. 2010), supporting the conclusion that color of the beak spot may be under sexual selection in both sexes. Such homogamy for color components of the beak spot was also observed in early breeders of another colony (Baie du Marin, Possession Island, Crozet Archipelago: Dobson et al. 2008); from this result it was surmised that colors of the beak spot might be of importance in both sexes, although the pairing process was not followed. In the

present study, we focused on the pairing process of early breeders and our results support the previous suggestions of mutual mate choice. Moreover, it does not seem that members of pairs that separated became late breeders: most of them found a new partner and produced an egg by mid-January (I. Keddar, unpublished data). Hence, a replication of this study with additional capture of new partners should also reveal homogamy for colors of the beak spot between members of the newly formed pairs.

The mutual mate choice hypothesis has been supported several times through the demonstration of assortative mating for secondary sexual traits (reviewed in Kraaijeveld et al. 2007). In some species, mutual ornaments seem to mediate interactions for both sexual and non-sexual resources (e.g. curled feather number in the black swan *Cygnus atratus*: Kraaijeveld et al. 2004; size of the carotenoid-based breast patch in the rock sparrow *Petronia petronia*: Griggio et al. 2005). However, it is not known if king penguins' beak spot plays a role in competition for resources other than mates. The size of the auricular patch seems to have a social function in both sexes (Viera et al. 2008) and a sexual function mainly in males (Jouventin et al. 2008; Pincemy et al. 2009; Nolan et al. 2010; Dobson et al. 2011): individuals expressing the largest auricular ornaments were the most aggressive, and males with experimentally reduced patches (within their natural range of variation) needed more time to find a mate. Even without a male preference for females with the largest ear patches, homogamy for the size of the auricular patch could still be expected if the most aggressive - and thus most ornamented- females could mate with the most ornamented males. Recent results, however, showed that intrasexual selection via aggressive contests is strongly biased toward male king penguins and that female-female fights for males, if any, are rare (Keddar et al. 2013). Thus, our results do not support the prediction of homogamy for the size of the auricular patch and, in accordance with previous studies, support the claim that this trait is not under mutual sexual selection (Pincemy et al. 2009; Dobson et al. 2011).

Difference in color ornaments between members of temporary and definitive pairs

Females that stayed with their initial partner expressed a beak spot more strongly UV in hue than females that separated from their initial partner, but this difference was not observed in males. This result suggests a selection of UV color of the beak spot of females, but does not provide evidence of selection of UV color of the beak spot of males. This is surprising, especially since previous experimental results suggesting slightly stronger selection on male UV color than on female UV color (Nolan et al. 2010). Thus, at first sight, our results and those of Nolan et al. (2010) might seem contradictory. However, individuals

studied in previous work were at the very beginning of the pair formation process (solitary individuals performing courtship calls; Nolan et al. 2010). In the present study, individuals observed were involved in displaying pairs that had learned each other's call: in other words, they were at a later stage of the pair formation process. Thus a possible explanation is that the strength of mate choice in each sex vary with the stage of the pairing process, with call learning acting as a separation between two stages: while females would be highly choosy with the male whose they learn the call, males would rather secure a first mate (in our colony, intrasexual selection is biased toward males; Keddar et al. 2013), and switch to a better option only if they have the opportunity. Another explanation of the discrepancy between our results and those of Nolan et al. (2010) is that the relative intensity of sexual selection on UV color of the beak spot experienced by the sexes changes across years. As recently emphasized, sexual selection can fluctuate in strength, direction, and form due to spatial and temporal environmental heterogeneity (Cornwallis & Uller 2010). In all cases, this suggests that observations of the mating process over a longer timespan would help to elucidate the underlying dynamic of the maintenance of UV and orange colors of the beak spot in both sexes.

In previous studies, males with experimentally reduced auricular patches (within their natural range of variation) needed more time to pair with a mate (Jouventin et al. 2008; Pincemy et al. 2009; Nolan et al. 2010). It is thus surprising that our results did not identify any influence of the size of this ornament on the male pairing process. Given that the sexual function of this trait has been observed in several different years and in both the Crozet and Kerguelen archipelagos, it seems unlikely that its influence on male pairing process greatly varies from year to year. Rather, we suggest that the size of this ornament may play a role during the early steps of the pairing process, when solitary males perform courtship calls, and that no noticeable selection occurs once pair members have learned each other's call (see above). The color of this ornament was not found to play a role in competition for mates in this study. Auricular color also does not appear too important to initial pairing by either sex, beyond indicating that an individual is a full adult and thus ready to mate (Nicolaus et al. 2007; Pincemy et al. 2009).

Condition dependence and honest signaling

We found that auricular width significantly reflected body mass and condition among the overall sample of penguins. Moreover, previous results suggest that hue of the breast plumage of male king penguins reflects the strength of their innate immune system (Nolan et

al. 2006). The potential importance of these ornaments during the early steps of pairing (i.e. before potential pair members learn each-other call), as well as the possibility of selection only under particular environmental conditions (Cornwallis & Uller 2010), provide alternative explanations for the associations of mass and condition with auricular width.

Little is known about the informative content of the multiple ornaments expressed by male and female king penguins. It is not known, for example, how parental ability is signaled. In the related and mutually ornamented yellow-eyed penguin *Megadyptes antipodes*, both sexes invest on average 5 months in parental care to successfully fledge their offspring (Darby & Seddon 1990; Williams 1995), and parental quality is reflected in eye and head plumage coloration (Massaro et al. 2003). Given the extensive period of biparental care in king penguins (14 to 16 months; Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996), we might also expect signaling of parental ability. Investigation of aspects of mate quality - besides body condition- that are signaled through male and female ornaments would improve our understanding of the maintenance of king penguins' secondary sexual traits.

Conclusion

In accordance with previous findings, we found evidence in support of mutual mate choice of UV color of the beak spot. Interestingly however, our results suggest that females experienced stronger sexual selection than males. This finding swims against the tide of previous results on sexual selection in king penguins, and future studies exploring how the strength of mate choice in each sex vary between years and/or with the stage of the pairing process should bring a better understanding of the maintenance of king penguins' mutual ornaments.

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4. Conspicuousness of color ornaments correlates with territory quality in the mutually ornamented king penguin, *Aptenodytes patagonicus*

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Males and females of some avian species express mutual colorful traits. According to social selection theory, this mutual ornamentation can be evolutionarily favored by competition for sexual and non-sexual (e.g. food, territory) resources occurring in both sexes. Many seabird species are mutually ornamented, but most studies have focused on competition for mates. In the present work, we tested the existence of relationships between mutual ornaments expressed by male and female king penguins and the quality (i.e. central or peripheral) of the territory where they settled for breeding. Both sexes exhibit yellow-orange auricular patches, a patch on the breast that grade from brown to bright yellow, and UV-orange beak spots. Most of these traits were associated with the location of the pair's breeding site within the colony. In addition, we found a tendency for the strength of some of these relationships to differ between males and females. Overall, our results suggest that taking into account competition for resources other than mates would prove insightful for understanding the maintenance of mutual ornamentation in king penguins and perhaps for mutually ornamented seabirds in general.

4.1. Introduction

The striking diversity and conspicuousness of avian ornamental traits has intrigued biologists since the second half of the 19th century (Darwin 1859, 1871; Wallace 1889, 1891; see Andersson 1994 and Hill & McGraw 2006 for recent reviews). According to social selection theory (Crook 1972; West-Eberhard 1979, 1983; Wolf et al. 1999; Lyon & Montgomerie 2012; Tobias et al. 2012), individuals expressing the most conspicuous ornamental traits are expected to be favored over less ornamented conspecific rivals when competing for access to resources such as food (Chaine et al. 2011; Santos et al. 2011), territories (Santos et al. 2011), or mates (*sexual selection*: Darwin 1871; Andersson 1994; Amundsen & Parn 2006; Hill 2006; Clutton-Brock 2009; Lyon & Montgomerie 2012). Hence, competitive social interactions are the cornerstone of social selection theory. Competition for mates has been extensively studied, and the common pattern where male ornamental traits attract mate selection by female partners has now an overwhelming support (Andersson 1994; Hill 2006). Most of these researches, however, focused on sexually dimorphic species. Interest in the maintenance of ornamental traits in both males and females (*mutual ornamentation*: Kraaijeveld et al. 2007) has grown, however, and several empirical studies suggested that maintenance of conspicuous traits expressed by both sexes is best understood when taking into account competition for sexual *and* non-sexual resources (reviewed in Tobias et al. 2012).

Mutual ornamentation has been studied in seabirds (Least auklet *Aethia pusilla*: Jones & Montgomerie 1992; Crested auklet *Aethia cristatella*: Jones & Hunter 1993; Inca tern *Larosterna inca*: Velando et al. 2001; Great cormorant *Phalacrocorax carbo*: Childress & Bennun 2002; European shag *Phalarocorax aristotelis*: Daunt et al. 2003; Yellow-eyed penguin *Megadyptes antipodes*: Massaro et al. 2003; Blue-footed booby *Sula nebouxii*: Torres & Velando 2003, 2005; King penguin *Aptenodytes patagonicus*: Pincemy et al. 2009, Nolan et al. 2010; Roseate tern *Sterna dougalii*: Palestis et al. 2012), although emphasis has been placed on mutual sexual selection (but see Jones 1990; Jones & Hunter 1999; Viera et al. 2008). The great majority of seabirds are colonial breeders, that is, species that breed in densely distributed territories containing no other resources than nest sites (Danchin & Wagner 1997).

The central-periphery distribution model proposed by Coulson (1968) suggested that for colonial species, central territories are of better quality than peripheral ones and provide the highest breeding success to pairs occupying them. Birds breeding in the center of the

colony are expected to have higher reproductive success than birds breeding at the periphery of the colony, due primarily to lower predation (Hamilton 1971). Hence during territory establishment, the high density of individuals seeking nesting sites of high quality should lead to frequent agonistic interactions within a colony, and create selection favoring traits that influence the outcome of such interactions (Wolf et al. 1999). Ornaments that influence the outcome of social interactions are precisely the sorts of traits that might be influenced by such social selection. While studies of sexually dimorphic passerine birds have supported this idea (see Santos et al. 2011 and Tobias et al. 2012 for recent reviews), little is known about the potential relationships existing between territory quality and ornamental traits expressed by mutually ornamented seabirds (but see Viera et al. 2008).

The king penguin is a mutually ornamented seabird breeding in colonies distributed throughout the sub-Antarctic islands. Territory acquisition occurs just after pair formation, which occurs between mid-November and mid-December for early breeders (Stonehouse 1960; Weimerskirch 1992; Descamps et al. 2002). Both pair members defend their small territory of approximately 0.5m² against neighbors and intruders for approximately 3 months (i.e., from laying of the single egg to chick emancipation), and peripheral individuals experience about twice as many interactions with predators as central ones (Cote 2000). In addition, levels of aggression are high, with incubating individuals experiencing an average rate of 38 aggressive interactions per hour and brooding individuals an average rate of 68 aggressive interactions per hour. As such, it has been suggested that the size of auricular patches expressed by males and females may be involved in the mediation of aggressive interactions. In a pioneering observational study, Viera et al. (2008) found that individuals that were more aggressive towards their conspecifics exhibited the largest auricular ornaments (i.e. patches of yellow-orange feathers) and defended the most central territories.

Besides their two auricular patches, male and female king penguins also exhibit a patch of feathers on the breast that grades from brown at the throat to bright yellow on the breast, and an orange and ultra-violet spot on each side of the lower mandible (Jouventin 1982; Dresp et al. 2005; Jouventin et al. 2005; Dresp & Langley 2006; McGraw et al. 2007; Dobson et al. 2008; Jouventin et al. 2008; Pincemy et al. 2009; Nolan et al. 2010; Dobson et al. 2011). All but one (Viera et al. 2008) of the previous studies of the function of king penguins' mutual ornaments focused on sexual selection: the color of the beak spot has been implicated in mutual mate choice (Dobson et al. 2008; Nolan et al. 2010; Keddar et al. unpublished data), and the size of male auricular patches favored access to females (Pincemy

et al. 2009; Nolan et al. 2010; thus male auricular patch size would have a function in both competition over sexual and non-sexual resources).

The aim of our study was to test the importance of king penguin's mutual ornaments and territory quality. Central territories were viewed as those of the highest quality and those at the periphery as less suitable ones, according a gradient of risk of egg or chick loss due to predation (Cote 2000), which should decrease from the periphery to the center of the colony (i.e. the domain of danger of each individual does not change as long as they stay at the same place: Hamilton 1971, p. 303). We tested two expectations. First that if individuals expressing the most conspicuously colored ornaments establish on the best territories, the degree of conspicuousness of the sampled individuals should exhibit a positive spatial correlation with the distance at which they established their territory from the edge of the colony. Second that if both sexes invest equally in territory defense (Cote 2000; Viera et al. 2008), no sex-differences should be observed in the strength or direction of relationships observed.

4.2. Methods

We studied a king penguin colony of about 100 000 pairs (Chamaille-James et al. 2000) at Cap Ratmanoff, Kerguelen Islands (49°12'S, 70°33'E), from 19 November 2010 to 10 December 2011. We followed 24 marked pairs of king penguins from courtship to territory establishment (i.e. laying). Before capturing a displaying pair, we ensured that both members had learned each other's call and would thus easily reunite if separated (e.g., subsequent to release after being measured). This was accomplished by slowly walking between displaying pairs so that visual contact between the pair was lost, and then observing them reunite by calling and walking back into close association. A hood was placed over each bird's head immediately after capture, and kept throughout the handling period (about 20 minutes for each pair).

Individuals were weighted to the nearest 0.1 kg with an electronic balance. Auricular width and inter-auricular distance were measured to the nearest 0.1 mm with a caliper. One hundred microliters of blood were drawn from of a brachial vein of each individual and preserved in Queen's buffer for later molecular sexing (Fridolfsson & Ellegren 1999). We measured color of the beak spot, and of the auricular and breast patches ("feather ornaments") using a USB2000 spectrophotometer and a PX2 pulsed-xenon light, calibrated against a WS-1 spectralon white standard (Ocean Optics Inc., Dunedin, FL, U.S.A.). Measurements were taken with the probe held at 90° to the ornaments. Each ornament was measured three times

and spectra were averaged using Avicol 6.0 (Gomez 2006). After handling, the two members of a pair were released at the point of capture.

Each bird was temporary marked with a black numbered band of white TESA tape (25 mm large) placed around each flipper, and these numbers were subsequently easily visible using binoculars during surveys of the colony. Censuses of all marked penguins, including identity, behavior, location, presence of a partner, and laying date were recorded twice each day, at about 6:00 and 18:00. Bands were removed after the field study.

The surface area of the colony has been estimated at 240 000 m² (Chamaille-Jammes et al. 2000). For practical reasons, however, we surveyed a smaller area of 4800 m² (120*40 m; figure 1). We installed visual markers every 10 m within this area using natural conspicuous materials (e.g., bones of long finned pilot whales *Globicephala melas*) before breeding pairs started to establish their territories, which allowed us to record the position of laying for each marked pair within a "natural grid" that produced minimum disturbance to the colony. All of the 24 pairs that we followed were captured at the east side of the colony (i.e. between colony edge and the ocean, where most mating displays occur; figure 1), and established within the grid. We considered the distance from the center to the edge (20 m) as an increasing gradient of risk of egg or chick loss due to predation (see introduction).

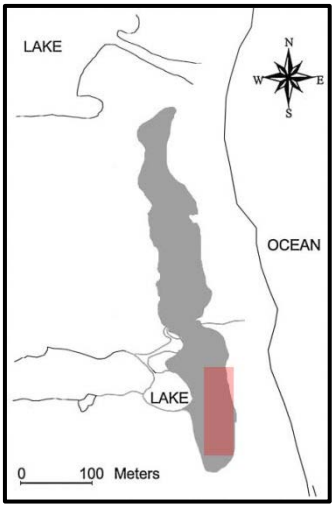

Figure 1. The king penguins colony of Cap Ratmanoff. In grey is the surface occupied by breeding pairs. In red is the "natural grid" surveyed during the daily census. Figure modified from Chamaille-James et al. 2000.

Color analysis

Light reflectance spectra ranged from 300 nm to 700 nm, and tristimulus color variables (i.e. hue, saturation, and brightness) were calculated (Montgomerie 2006). Hue corresponds to what is commonly called "color". Saturation is a measure of spectral purity, and indicates the degree to which a color appears as composed of single wavelength. This measure has been related to the pigment content of ornaments in a few species (e.g. yellow feathers of Snares penguins *Eudyptes robustus*: McGraw et al. 2009; beaks of mallard *Anas platyrhynchos*: Butler et al. 2011). Brightness is a measure of spectral intensity, and indicates the total amount of light reflected by an ornament.

Hue of the feather ornaments was calculated as the wavelength at which the reflectance was halfway between its maximum and minimum values (formulae H_3 from Montgomerie 2006). Saturation of the feather ornaments was calculated as the difference between maximum and minimum reflectance across the whole spectrum, divided by the mean brightness of the spectrum (formulae S_8 from Montgomerie 2006). Mean brightness of the feather ornaments was calculated as the sum of the reflectance values between 300 and 700 nm, divided by the number of values (i.e. sampling points) across the whole spectrum (formulae B_2 from Montgomerie 2006). Due to the bimodal distribution of beak spot color reflectance, we split the spectrum of this ornament in half and defined an ultraviolet (UV) part between 300 and 499 nm and a yellow-orange part between 500 and 700 nm (figure 2). UV saturation and mean brightness, as well as yellow-orange hue, saturation and mean brightness of this ornament were calculated following the same principles as for feather ornaments, except that the range of computation was restricted to 300-499 nm for the UV and to 500-700 nm for the yellow-orange. Finally, UV hue of the beak spot was calculated as the wavelength at maximum reflectance between 300 and 499 nm.

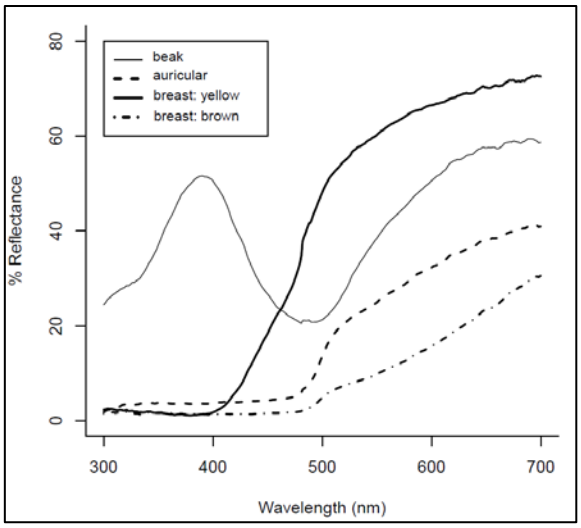

Figure 2. Example of reflectance spectra of the beak spot, auricular patch, brown part of the breast patch, and yellow part of the breast patch. The vertical dotted line show the separation between the bell-shaped UV reflecting part of the beak spot (300-499 nm) and the orange reflecting part of the beak spot (500-700 nm).

Statistical analyses

All analyses were performed using R 2.15.2 (R core team 2012). Relationships between the distance at which pairs established their territories from the edge of the colony and morphometric/color measures were assessed using linear models with distance from the edge, sex, and interaction between sex and distance as fixed effects.

The dataset was preliminarily examined for outliers using Dixon's Q test (Sokal & Rohlf 1995, p. 406). One outlier was found for brown saturation of male breast patch ($Q = 0.63$, $P < 0.0001$). Two outliers were also found for orange hue of male and female beak spots (respectively: $Q = 0.73$, $P < 0.0001$, and $Q = 0.56$, $P = 0.009$). These 3 extreme data points were censored when necessary, yielding more conservative results.

4.3. Results

Auricular patches

Males expressed larger auricular patches than females (male intercept ± s.d. = 34.8 mm ±1.0; female intercept ± s.d. = 31.3 mm ±1.1; $t_{1,45} = 3.47$, P = 0.001; figure 3); in both sexes, this trait was significantly associated with the distance at which the territory was established from the edge of the colony (slope ± s.d. = 0.19 ±0.09; $t_{1,45} = 2.09$, P = 0.042; figure 3). Interaction between sex and distance was not significant ($t_{1,44} = 0.36$, P = 0.72). No significant relationships were observed between the distance at which male or female individuals established their territory from the edge of the colony and hue, saturation, or brightness of their auricular patches (all $P \geq 0.28$).

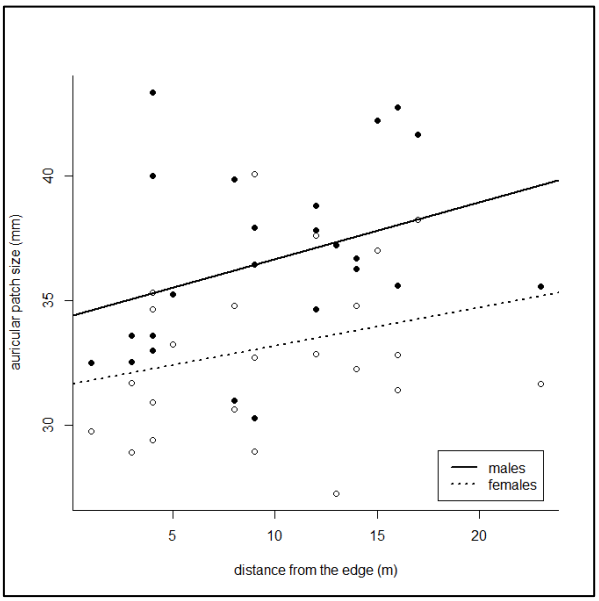

Figure 3. Relationship between the distance at which males (black dots) and females (open circles) established there territory from the edge of the colony and the size of their auricular patches.

Breast patch

Hue of the brown part of the breast patch was nearly significantly higher in females than in males (female intercept ± s.d. = 576.1 nm ± 4.2; male intercept ± s.d. = 569.0 nm ± 3.7; $t_{1,45}$ =-1.9, P = 0.062; figure 4a); in both sexes, this trait was significantly associated with the distance at which the territory was from the edge of the colony (slope ± s.d. = 0.67 ±0.33; $t_{1,45}$ = 2.00, P = 0.051; figure 4a). Interaction between sex and distance was not significant ($t_{1,44}$ = 0.36, P = 0.9). No significant effects were observed for the hue of the yellow part of the breast (intercept: $t_{1,45}$ = -0.12, P = 0.9; slope: $t_{1,45}$ = 1.43, P = 0.16; interaction: $t_{1,44}$ = -0.76, P = 0.45).

Saturation of the brown part of the breast was significantly associated with the distance at which the territory was from the edge of the colony ($t_{1,43}$ = 2.80, P = 0.008). However, interaction between sex and distance was nearly significant and suggested that this relationship was mainly due to the effect of the brown saturation of female breast patch (female slope ± s.d. = 0.019 ± 0.007; male slope ± s.d. = 0.002 ± 0.009; $t_{1,43}$ = -1.75, P = 0.088; figure 4b). Intercepts were not significantly different between the sexes ($t_{1,43}$ = 0.99, P > 0.32). Saturation of the yellow part of the breast patch was significantly associated with the distance at which the territory was established from the edge of the colony in both sexes (slope ± s.d. = 0.0063 ± 0.003; $t_{1,45}$ = 2.43, P = 0.019; figure 4c). Intercepts were not significantly different between the sexes ($t_{1,45}$ = -0.43, P = 0.67), and no significant interaction was observed ($t_{1,44}$ = -1.4, P = 0.17).

Brightness of the brown part of the breast was significantly negatively associated with the distance at which the territory was from the edge of the colony in both sexes (slope ± s.d. = -0.25; $t_{1,45}$ = -3.17, P = 0.003; figure 4d). Intercepts were not significantly different between the sexes ($t_{1,45}$ = -0.01, P = 0.9), and no significant interaction was observed ($t_{1,44}$ = 0.05, P = 0.9). No significant effect were observed for the brightness of the yellow part of the breast (intercept: $t_{1,45}$ = -1.08, P = 0.28; slope: $t_{1,45}$ = 1.75, P = 0.087; interaction: $t_{1,44}$ = 0.67, P = 0.51). The statistical effect of the slope, however, was nearly significant and exhibited a pattern qualitatively similar as the pattern observed for the brightness of the brown part of the breast (figure not shown).

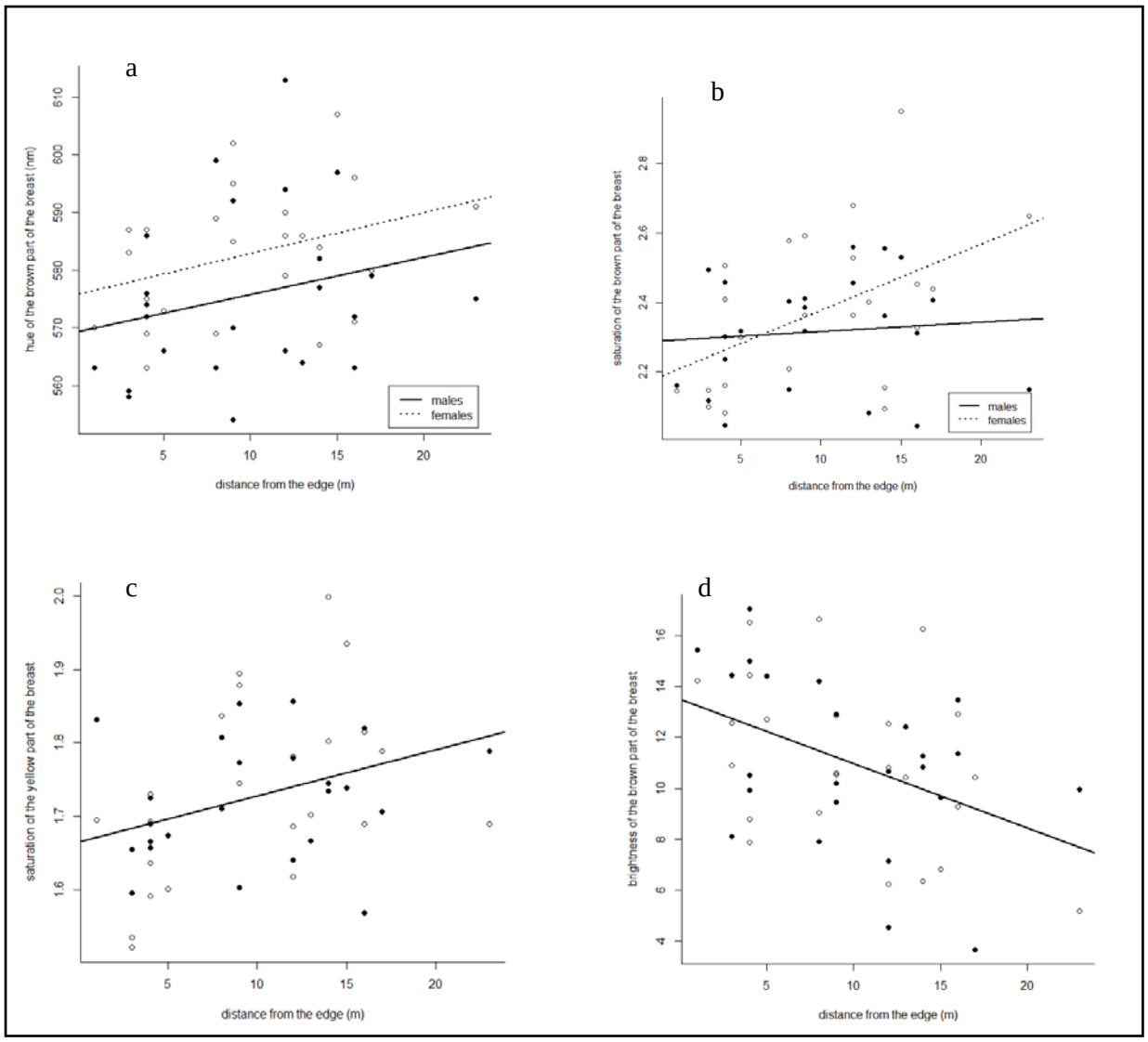

Figure 4. Relationships between the distance at which males (black dots) and females (open circles) established there territory from the edge of the colony and (a) brown hue, (b) brown saturation, (c) yellow saturation, (d) brown brightness of the breast patch.

Beak spot

Hue of the orange reflecting part of the beak spot was significantly associated with the distance at which the territory was established from the edge of the colony ($t_{1,42}$ = 2.67, P = 0.011). However, interaction between sex and distance was nearly significant and suggested that this relationship was mainly due to the effect of the orange hue of female beak spot (female slope ± s.d. = 0.29 ± 0.11; male slope ± s.d. = -0.001 ± 0.15; $t_{1,42}$ = -1.89, P = 0.066; figure 5a). Intercepts were not significantly different between the sexes ($t_{1,42}$ = 1.67, P = 0.10).

No significant relationships were observed between the saturation of the orange reflecting part of the beak spot and the distance at which the territory was established from the edge of the colony ($t_{1,45}$ = -1.20, P = 0.24) and no significant interaction were observed ($t_{1,44}$ = -0.71, P = 0.48). Males, however, expressed a beak spot more saturated than females (male intercept ± s.d. = 0.72 ± 0.04; female intercept ± s.d. = 0.64 ± 0.03; $t_{1,45}$ = 2.14, P = 0.038). No significant effects were observed for orange brightness of the beak spot (intercept: $t_{1,45}$ = -1.07, P = 0.29; slope: $t_{1,45}$ = 1.02, P = 0.31; interaction: $t_{1,44}$ = 0.37, P = 0.71).

Male beak spots reflected toward lower UV wavelengths than female beak spot (male intercept ± s.d. = 379 nm ± 2.6; female intercept ± s.d. = 386 nm ± 3.0; $t_{1,45}$ = - 2.82, P = 0.007). No statistically significant effect was observed for the slope ($t_{1,45}$ = 1.27, P = 0.21) and no significant interaction was observed ($t_{1,44}$ = -0.067, P = 0.95). In both sexes, UV saturation of the beak spot was nearly significantly associated with the distance at which the territory was established from the edge of the colony (slope ± s.d. = -0.0067 ± 0.003; $t_{1,45}$ = -1.97, P = 0.055; figure 5b). Interaction between sex and distance was not significant ($t_{1,44}$ = 0.19, P = 0.85). Males, however, expressed a more saturated beak spot than females (male intercept ± s.d. = 0.88 ± 0.038; female intercept ± s.d. = 0.76 ± 0.043; $t_{1,45}$ = 2.83, P = 0.007; figure 5b). Finally, no significant effects were observed for UV brightness of the beak spot (intercept: $t_{1,45}$ = -1.3, P = 0.20 ; slope: $t_{1,45}$ = 0.98, P = 0.33; interaction: $t_{1,44}$ = 0.41, P = 0.68).

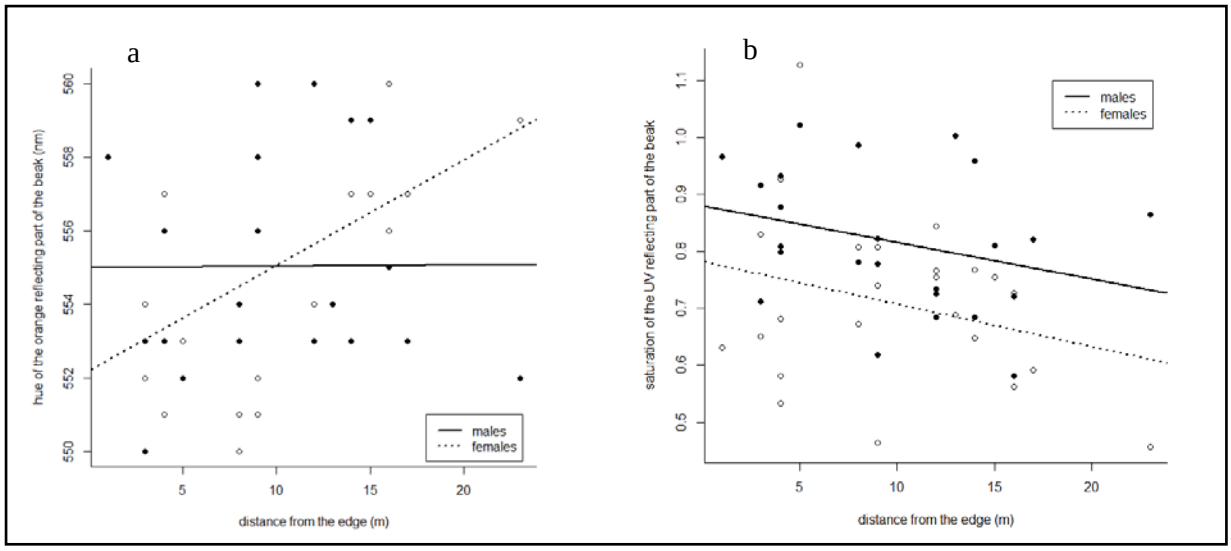

Figure 5. Relationships between the distance at which males (black dots) and females (open circles) established there territory from the edge of the colony and (a) orange hue, (b) UV saturation of the beak spot.

4.4. Discussion

Main results

The first aim of our study was to test the existence relationships between territory quality and mutual ornaments expressed by male and female king penguins. Our second aim was to test for sex-differences among the relationships which were found to exist. We observed that in both sexes, the size of auricular patches, hue of the brown part of the breast patch, and saturation of the yellow part of the breast patch were positively associated with the distance at which the territory was established from the edge of the colony; brightness of the brown part of the breast patch and UV saturation of the beak spot were negatively associated with distance from the edge of the colony. In addition, saturation of the brown part of the breast patch and orange hue of the beak spots were positively associated with the distance from the edge of the colony in females but not in males.

Our moderate sample size led to several P-values being near the critical threshold. This work, however, is the first to undertake the study of relationships between colors of mutual ornamentation and territory quality in a seabird species and as such, we have chosen to be slightly more tolerant with acceptance of statistically significant effects. Our results call for further work, and future studies may help to support or moderate some of our interpretations (see below).

Spatial variation of territory quality

The central-periphery model of spatial nest distribution has been studied in several seabird species; some studies supported this model (e.g. Laughting gull *Leucophaeus atricilla*: Montevecchi 1978; Magellanic penguin *Spheniscus magellanicus*: Gochfeld 1980; Black-legged Kittiwake *Rissa tridactyla*: Aebischer & Coulson 1990; Cape Gannet *Morus capensis*: Staverees et al. 2008; Royal tern *Thalasseus maximus*: Angulo-Gastelum et al. 2011), while other not (e.g. European shag *Phalacrocorax aristotelis*: Velando & Freire 2001; Brown Booby *Sula leucogaster*: Ospina-Alvarez 2008; King penguin: Descamps et al. 2009). In a comparison of 19 seabird species, patterns of spatial variability of nest-site quality appeared to influence patterns of distribution of breeding pairs (see table 3 in Velando & Freire 2001). For example, an homogenous risk of predation across a whole colony could favor a central-periphery distribution of pairs, while a patchy distribution of the risk of predation (e.g. if topographical features of the habitat offer nesting positions more sheltered than other) could favor a central-satellite distribution of breeding pairs. That is, in the former case high quality individuals would occupy central territories at the scale of the whole colony and thus nest close together, while in the latter case high quality individuals would follow a patchy distribution and be surrounded by lower quality individuals (Velando & Freire 2001).

While the comparison made by Velando & Freire (2001) focuses mainly on interspecific differences, we could also expect the existence of intraspecific differences if different populations occupy habitats presenting different characteristics (see also discussion in Ospina-Alvarez 2008). Behavioral studies conducted in king penguins focus mainly on the colony of *La Baie du Marin* on the Crozet Archipelago (e.g. Cote 2000; Viera et al. 2008) and on the colony of *Cap Ratmanoff* on the Kerguelen Archipelago, each having its own characteristics. The colony of *La Baie du Marin* consists of about 16000 pairs established on an area characterized by a relatively complex feature of risks of flooding, tick infestation, predation pressure, topographic slope, and scientific installations (see Descamps et al. 2009 and references therein for a detailed description). The colony of *Cap Ratmanoff* consists of more than 100 000 pairs established on a relatively flat ground farther from the sea than the colony of *La Baie du Marin*, and is thus much less exposed to flooding (I. Keddar, F. Bonadonna & F. S. Dobson, personal observations; see also figure 1 in Descamps et al. 2009 and figure 1 in this study). In addition, tick infestation at the colony of *Cap Ratmanoff* seems lower than at the colony of *La Baie du Marin* (C. Le Bohec, personal communication). The colony of *Cap Ratmanoff* has yet to be described as precisely as the colony of *La Baie du Marin*, but preliminary observations suggest that their only similarity is that birds established

on peripheral territories are exposed to higher predation pressures than birds established on central territories (Cote 2000; Descamps et al. 2005; I. Keddar, F. Bonadonna & F. S. Dobson, personal observations). Therefore, studying the relationship between territory quality and conspicuousness of mutual color ornaments in different colonies may shed light on geographical differences that would be insightful for our understanding of the maintenance of king penguin's colorful traits.

Mutual color ornaments and territory quality

Similarly as a previous study conducted in the colony *La Baie du Marin* (Viera et al. 2008), we observed that members of pairs occupying central territories expressed larger auricular patches than individuals occupying peripheral territories. In addition, we found that the brown part of the breast patch of more central pairs reflected toward longer wavelengths and that the yellow part of their breast patch was more saturated. Albeit these traits may be related to levels of aggressiveness similarly as it was observed by Viera et al. (2008) for the size of auricular patches (see also Jones 1990; Jones & Hunter 1999), the causal path leading to this spatial distribution would require formal experimental testing (field research in progress). Some support for this hypothesis has been found in the scarlet-tufted sunbird *Nectarinia johnsoni*, where males with experimentally increased ornaments (red pectoral tufts) experienced less aggressiveness from conspecifics and were able to defend territories of better quality, while males with experimentally decreased ornaments experienced more aggressiveness from conspecifics and defended territories of lower quality (Evans & Hatchwell 1992).

We also observed a negative association between the distance at which territories were from the edge of the colony and both brightness of the brown part of the breast patch and UV saturation of the beak spots. While the relationship involving brown brightness could be explained by its negative correlation with brown hue and brown saturation (Dobson et al. 2008; I. Keddar et al., unpublished data; this study, data not shown), the negative relationship involving UV saturation is actually hard to explain. Indeed, UV signal of the beak spot has been suggested to be involved in mutual mate choice (Nolan et al. 2010; I. Keddar et al., unpublished data). A complex interaction between competition for mates and competition for territories might occur.

Sex-differences in ornament expression with respect to territory location

A recent meta-analysis in mutually ornamented species reported that globally, female ornaments are more commonly involved in competition for non-sexual than sexual resources, while the reverse was true for males (Tobias et al. 2012). Our observations that saturation of the brown part of the breast patch and orange hue of the beak spots were positively associated with the distance from the edge of the colony in females but not in males may fit with this general trend, although an explicit support would require study of levels of aggressiveness and movement of standing breeders through the colony.

Previous studies conducted at *La Baie du Marin* reported that investment in territory defense was roughly the same in both sexes (Cote 2000; Viera et al. 2008), and in regard to these results, the sexes differences we observed in the present study might appear surprising at first sight. However, as emphasized by Stutchbury (1992) in a study of territory defense in the purple martin *Progne subis*, defense is only one component of territoriality. That is, birds must first obtain a territory to defend (see Stutchbury 1992 and references therein). Hence, while both male and female king penguins might invest equally in territory defense, the sex differences that we observed may suggest a greater involvement of females in initial territory acquisition. Little is known about how king penguins select their habitat, except that they seem highly philopatric (Bried & Jouventin 2001; A. P. Nesterova, personal communication). However, divorce rate from one breeding season to another is also high (range 63%: Toscani et al. in prep.). Therefore, if both sexes are equally philopatric a potential conflict may be at stake between pair members of one breeding season and of the following one. A potential resolution of this conflict could be found in a female-biased philopatry coupled to a higher propensity of males to seek for mates in a larger area of the colony. This statement remains speculative, but suggest nonetheless exciting avenue for future researches.

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5. Variation of mutual color ornaments and mutual mate choice in response to winter resources availability in a mutually ornamented seabird

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Keywords: king penguin, *Aptenodytes patagonicus*, early breeding, mutual ornamentation, mutual mate choice

Sexual selection is a major evolutionary force. However, our understanding of this process remains in some cases limited because little is known about how temporal changes in environmental conditions influence it, especially in mutually ornamented seabird species. The aim of our study was to investigate inter-annual changes in color ornaments and mate choice, body mass, and delay to lay in the multiply and mutually ornamented king penguin by comparing these traits in a year when winter food resources were abundant to a year when resources were scarce. We observed that displaying birds started their breeding cycle with a similar body mass each year, but expressed globally lower conspicuous ornaments when they spent the preceding winter under resources stress. In addition, comparison of the mating process suggested lower levels of choosiness in both sexes during the unfavorable year, perhaps in order to pair quicker and partly compensate the delay with which they entered in reproduction.

5.1. Introduction

Sexual selection theory aims at explaining the evolution and maintenance of secondary sexual traits expressed by males and/or females of sexual species (Darwin 1871; Andersson 1994; Tobias et al. 2012, and references therein). In many species, individuals compete for access to mating partners. Selection of secondary sexual traits occurs when their expression is associated with heritable differences in mating success (Danchin & Cezilly 2007). Such differences can arise from two mechanisms: the first encompasses all situations involving interactions between same-sex individuals (*intrasexual selection*; e.g. male fights in elephant seals, *Mirounga sp.*: Hoelzel et al. 1999), while in the second same-sex interactions are mediated by opposite-sex individuals (*intersexual selection*; e.g. female mate choice in long-tailed widowbirds, *Euplectes progne*: Andersson 1982). Ornamental colors are among the most studied secondary sexually traits, especially in birds (Griffith & Pryke 2006), and maintenance of colorful male traits through female choice has now overwhelming empirical support (Hill 2006). Most of these researches, however, focused on sexually dimorphic species.

Recently, the maintenance of sexually monomorphic color ornaments (*mutual ornamentation*: see Kraaijeveld et al. 2007 for a recent review) received a growing interest, particularly in seabirds (Great cormorant *Phalacrocorax carbo*: Childress & Bennun 2002; Least auklet *Aethia pusilla*: Jones & Montgomerie 2002; Yellow-eyed penguin *Megadyptes antipodes*: Massaro et al. 2003; King penguin *Aptenodytes patagonicus*: Nolan et al. 2010 and references therein). Two hypotheses have been proposed to explain the maintenance of ornamental monomorphism: (i) the *genetic correlation hypothesis* (Lande 1980; Lande & Arnold 1983), according to which ornaments are functional in one sex (usually males) and non-functional in the other (usually females), and (ii) the *mutual selection hypothesis*, according to which elaborate ornaments result from a selection for their expression in both sexes. Under this last scenario, such elaborate characters could result from competition over sexual and/or non-sexual resources (the "*social selection hypothesis*": West-Eberhard 1979, 1983; Wolf et al. 1999; Lyon & Montgomerie 2012). Mutual competition for sexual resources (the "*mutual mate choice hypothesis*": Huxley 1914) is theoretically expected in species exhibiting extensive biparental care and high mate encounter rate (Kokko and Johnstone 2002), and has empirical support in several species of seabirds (Kraaijeveld et al. 2007; Nolan et al. 2010).

In seabirds, as in many other avian species, pairs breeding early in the season have a higher reproductive success that pairs breeding later (Weimerskirch et al. 1992; Kokko 1999 and references therein; Dearborn & Ryan 2002). According to the Darwin-Fisher theory of sexual selection in monogamous birds, the relationship between breeding date and fecundity arises from the positive correlation of these two variables with nutritional condition (Price et al. 1988; Kirkpatrick et al. 1990). In Antarctic birds, however, a trend toward later arrival and later laying has been observed since 1950 (Barbraud & Weimerskirch 2006). This phenological change is thought to result from a time-shift in marine resource availability due to modifications of abiotic and biotic oceanographic conditions (Loeb et al. 1997; Nicol et al. 2000; Parkinson 2002; Atkinson et al. 2004; Barbraud & Weimerskirch 2006), causing seabirds to forage longer at sea in order to build up reserves necessary for breeding. This phenomenon is also thought to extend to the sub-Antarctic king penguin (Olsson 1995; Weimerskirch et al. 1992; Scheffer et al. 2013). During a 6 years survey of the king penguin's breeding cycle, reduced food availability lengthened foraging trips at sea (Olsson 1995), delayed the onset of egg laying (Olsson & Brodin 1997), reduced chick condition, and decreased post-fledging survival (Olsson 1997). Moreover, breeding males tend to interrupt courtship or desert their egg if male body mass falls below a critical threshold (Gauthier-Clerc et al. 2001). Thus, changes in marine resources availability, through an effect on body reserves, can impact the king penguin's breeding cycle. Little is known, however, about how these changes affect the mutual sexual selection process that occurs during the breeding season. For example, while the onset of the king penguin's breeding cycle is delayed during unfavorable years, the extent of the resulting delay in egg laying could be partly reduced if birds shorten their courtship period (see Barbraud & Weimerskirch 2006 for examples in Antarctic seabirds). Among seabirds, the king penguin has a long breeding cycle beginning in the austral spring, after the pre-nuptial molt (Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996; Descamps 2002). Both sexes invest 14-16 months in egg and chick care to successfully raise their single offspring, and chick survival over the winter depends on laying date and marine resource availability (Weimerskirsh 1992; Olsson 1996; Olsson 1997; Olsson & Brodin 1997).

Male and female king penguins exhibit two yellow auricular patches of feathers, an orange and ultra-violet spot on each side of the lower mandible, and a patch of feathers on the breast that grades from brown at the throat to bright yellow on the breast (Jouventin 1982; Dresp et al. 2005; Jouventin et al. 2005; Dresp & Langley 2006; Nolan et al. 2006; McGraw et al. 2007; Dobson et al. 2008; Jouventin et al. 2008; Pincemy et al. 2009; Nolan et al. 2010;

Dobson et al. 2011). Growing comparative and experimental evidence suggests that orange and UV colors of the beak spot are of interest to both sexes mate choice (Dobson et al. 2008; Nolan et al. 2010; Keddar et al. unpublished data). Also, experimental reduction of the size of the auricular patch delayed pairing, but only in males (Pincemy et al. 2009; Nolan et al. 2010). During courtship, individuals display to potential partners around the fringes of the colony, forming temporary pairs. Some of the temporary pairs become definitive and produce an egg, while in others pairs separate and perhaps switch to another potential partner (Olsson et al. 2001; Keddar et al. unpublished data). We surmised that if members of a temporary pair separated, one or both of them was perceived as unattractive, whereas if a temporary pair became a definitive one, each of its members was perceived as suitable for producing an egg and raising a chick.

The aim of our study was to investigate inter-annual changes in body mass, color ornaments, mate choice, and delay to lay in the multiply and mutually ornamented king penguin by comparing these traits in a year when winter food resources were abundant to a year when resources were scarce. These inter-annual differences were investigated through four expectations. First, body mass appears of critical importance to breeding, as it strongly constrains success. Males invariably take the first shift (15-21 days) standing with the single egg on their feet, and they must have sufficient body reserves to remain without feeding until the female partner returns from the sea to relieve them (Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996; Gauthier-Clerc et al. 2001; Descamps 2002). Thus, our first expectation was for a lack of notable differences in body mass between birds displaying for mates during the favorable year versus the unfavorable year, especially for males. Second, the joint constraints on body mass and early breeding should affect the amount of resources allocated to production of ornaments. Thus, we expected that color ornaments should be less conspicuous, either smaller or of less striking appearance, during the unfavorable year than during the favorable year. Third, it is a central tenet of sexual selection theory that the degree of expression of color ornaments reflects the quality of their bearer as potential mates (Zahavi 1975; Andersson 1994): thus, individuals with more developed color ornaments should pair quicker than birds with less developed ornaments (Kirkpatrick et al. 1990, p.189-190). Thus, in accord with previous studies of mate choice (Pincemy et al. 2009; Nolan et al. 2010), we expected that males and females involved in definitive pairs should express more colorful beaks, and males of those pairs should express larger ear patches than individuals involved in temporary pairs, in both years. Because more conspicuous ornaments should allow quicker

pairing, our fourth expectation was that although color ornaments might be globally less conspicuous during the unfavorable year, ornaments that are the most important for mate choice (i.e. UV color of the beak spot and size of auricular patches for males) should be maintained to a higher level of expression than ornaments less likely to be under the influence of sexual selection (i.e. colors of feather ornaments and size of female auricular patches). Because of the influence of coevolution of ornament expression and partner preference for expressive ornaments (viz., linkage disequilibrium of these traits), sexual selection on ornaments used in mate choice should be under particularly strong selection (Lande & Arnold 1983). Finally, we explored inter-annual differences in the role that mate choice has on the delay to lay an egg by comparing the time elapsed between the capture of birds and laying as well as the proportion of definitive *versus* temporary pairs each year.

5.2. Methods

Study area and data collection

We studied displaying pairs of king penguins at the colony of Cap Ratmanoff, Kerguelen Islands (49°12'S, 70°33'E), from 20 November to 12 December 2008 and from the 19 November 2010 to 25 January 2011. At the beginning of the 2008 season thousands of individuals were already incubating their egg and numerous pairs were settled within the colony (F.S. Dobson & C. Couchoux, personal observation). At the beginning of the 2010 season, only a few incubating individuals were observed, the colony occupied a smaller area, and many birds were still returning ashore to start breeding (F.S. Dobson & I. Keddar, personal observations). Moreover, overwinter survival of chicks at the onset of the 2008 breeding season (i.e. chicks that hatched in 2007 and were near fledging in 2008) was quite high (0.55; C.A. Bost, personal communication), while overwinter survival of chicks at the onset of the 2010 season was catastrophic (0.00; C.A. Bost, personal communication). Therefore, the 2008 season was revealed as a favorable year and the 2010 season was a year of unfavorable environmental conditions (see Olsson 1997; Olsson & Brodin 1997; Olsson & van der Jeugd 2002 for similar arguments).

Before capturing a displaying pair, we ensured that both members had learned each other's call and would thus easily reunite if separated (e.g., subsequent to release after being measured). This was accomplished by walking between displaying pairs, so that visual contact between the pair was lost, and then observing them reunite by calling and walking back into close association. A hood was placed over each bird's head immediately after

capture, and kept throughout the handling period (about 20 minutes for each pair), so that birds stayed calm.

Individuals were weighted to the nearest 0.1 kg with an electronic balance. Auricular width (a reasonable measure of auricular size; Dobson et al. 2011) and inter-auricular distance were measured to the nearest 0.1 mm with a caliper. One hundred microliters of blood were drawn from of a brachial vein of each individual and preserved in Queen's buffer for later molecular sexing (Fridolfsson & Ellegren 1999). We measured color of the beak spot, and of the auricular and breast patches ("feather ornaments") using a USB2000 spectrophotometer and a PX2 pulsed-xenon light, calibrated against a WS-1 white standard (Ocean Optics Inc., Dunedin, FL, U.S.A.). Measurements were taken with the probe held at 90° to the ornaments. Each ornament was measured three times and spectra were averaged using Avicol 6.0 (Gomez 2006). After handling, the two members of a pair were released at the point of capture.

Each bird was temporary marked with a numbered plastic band placed around each flipper, and these numbers were subsequently easily visible using binoculars during surveys of the colony. Censuses of all marked penguins, including identity, behavior, location, presence of a partner, and laying date were recorded twice each day, at about 6:00 and 18:00. Bands were removed after the field study of each year. We captured both members of 73 displaying pairs in 2008, and both members of 82 displaying pairs in 2010.

Color analysis

Light reflectance spectra ranged from 300 nm to 700 nm, and tristimulus color variables (i.e. hue, saturation, and brightness) were calculated to summarize them (Montgomerie 2006). Hue indicates which wavelengths contribute the most to the color signal emitted from an ornament of a sender, and partly determines the degree of activation of each cone type in the retina of a receiver (i.e. the perceived signal). It corresponds to what is commonly called "color". Saturation is a measure of spectral purity, and indicates the degree to which a color appears as composed of single wavelength. This measure has been related to the pigment content of ornaments in a few species (e.g. yellow feathers of Snares penguins, *Eudyptes robustus*, McGraw et al. 2009; beaks of mallards *Anas platyrhynchos*, Butler et al. 2011). Brightness is a measure of spectral intensity, and indicates the total amount of light coming from an ornament.

Hue of the feather ornaments was calculated as the wavelength at which the reflectance was halfway between its maximum and minimum values (formulae H_3 from Montgomerie 2006). Saturation of the feather ornaments was calculated as the difference

between maximum and minimum reflectance across the whole spectrum, divided by the mean brightness of the spectrum (formulae S_8 from Montgomerie 2006). Mean brightness of the feather ornaments was calculated as the sum of the reflectance values between 300 and 700 nm, divided by the number of values (i.e. sampling points) across the whole spectrum (formulae B_2 from Montgomerie 2006). Due to the bimodal distribution of beak spot color reflectance, we split the spectrum of this ornament in half and defined an ultraviolet (UV) part between 300 and 499 nm and a yellow-orange part between 500 and 700 nm (figure 1). UV saturation and mean brightness, as well as yellow-orange hue, saturation and mean brightness of this ornament were calculated following the same principles as for feather ornaments, except that the range of computation was restricted to 300-499 nm for the UV and to 500-700 nm for the yellow-orange. UV hue of the beak spot was calculated as the wavelength at maximum reflectance between 300 and 499 nm.

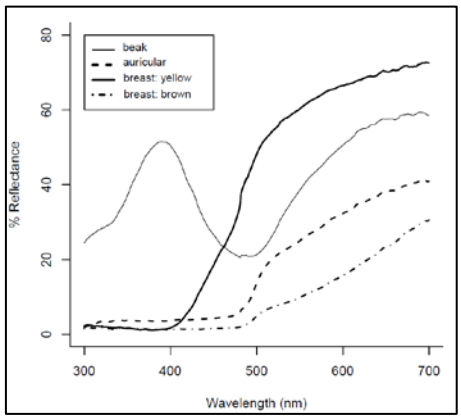

Figure 1. Example of reflectance spectra of the beak spot, auricular patch, brown part of the breast patch, and yellow part of the breast patch. The vertical dotted line show the separation between the bell-shaped UV reflecting part of the beak spot (300-499 nm) and the orange reflecting part of the beak spot (500-700 nm).

Statistical analyses

All statistical analyses were performed using R 2.15.2 (R core team 2012). Between-year and between-sex differences in body mass were tested with two-way anova. Mean values of hue, saturation, and brightness of each color ornament were compared between years using Student's t test when data were homoscedastic, and Welch's t test otherwise. Because we used several measures to characterize each ornament, Bonferroni corrections were applied to adjust the significance threshold. Auricular patch was characterized by 5 measures (tristimulus variables, auricular width, and inter-auricular distance): therefore, the significance level was

lowered to 0.05/5 = 0.01 (Sokal & Rohlf 1995; Montgomerie 2006, p. 133-134). The breast patch was characterized by 6 measures (tristimulus variables computed for the upper brown part and for the lower yellow part), thus the significance threshold was lowered to 0.05/6 = 0.008. The same procedure was applied for the beak spot (tristimulus variables computed separately for the UV and for the orange parts of the reflectance spectra). Mean inter-annual differences were quantified by computing an effect size statistic robust to heteroscedasticity derived from Cohen's d (Hereafter named *Robust d*; Wilcox & Tian 2011). Compared to the original Cohen's d, a *robust d* value of 0.15 corresponds to a small effect, 0.35 to a medium effect, and 0.5 to a large effect (Wilcox & Tian 2011). Preliminary analyses of the data revealed sexual dimorphism for size and color characteristics of the auricular patch. Thus, for this ornament inter-annual differences were studied separately for each sex. The influence of ornaments and body mass on the mate choice process was investigated by comparing these traits between individuals involved in definitive pairs and individuals involved in temporary pairs, each year and each sex separately, using Binomial models (table 1) and backward regression. Mean differences found to be significant were quantified by computing a robust d. We used Cox's proportional hazard models to investigate differences between temporary and definitive pairs as well as inter-annual differences in the time elapsed from capture to egg laying. Finally, the proportion of definitive and temporary pairs observed each year were compared with a chi^2 test.

Table 1. Binomial models used to study the influence of ornaments and body mass on the mate choice process, separately for each year and each sex. sat.: saturation; bri.: brightness; distance: inter-auricular distance.

			auricular	breast	beak
1.	status ~	mass +	hue + width + distance +	yellow hue + brown hue +	UV hue
2.	status ~	mass +	sat. + width + distance +	yellow sat. + brown sat. +	UV sat.
3.	status ~	mass +	bri. + width + distance +	yellow bri. + brown bri. +	UV bri.
4.	status ~	mass +	hue + width + distance +	yellow hue + brown hue +	orange hue
5.	status ~	mass +	sat. + width + distance +	yellow sat. + brown sat. +	orange sat.
6.	status ~	mass +	bri. + width + distance +	yellow bri. + brown bri. +	orange bri.

5.3. Results

Inter-annual differences in body mass in each sex

Males were on average 10 % heavier than females ($F_{1,306}$ = 164, n = 308, P < 0.0001; table 2). No significant differences in body mass were observed between years ($F_{1,306}$ = 0.96, n = 308, P = 0.33; table 2), and the interaction of sex and year was not significant ($F_{1,306}$ = 0.30, n = 308, P = 0.59).

Inter-annual differences in color ornaments

Male auricular patches were greater in hue (i.e., more yellow-orange than yellow) during the favorable year (table 3a, figure 2). Moreover, individuals of both sexes expressed larger and more saturated patches during the favorable year than during the unfavorable year; in both cases, the difference was slightly stronger in males than in females (table 3a, figure 3). No inter-annual differences were observed for the brightness of the auricular patch or for the inter-auricular distance, for either sex (table 3a, figure 4). Computation of effect size suggested moderate to large effects among the differences found to be significant (table 3a, figures 2, 3).

The yellow part of the breast exhibited a significantly lesser hue during the favorable year; an opposite pattern was observed for the brown part of the breast, although the difference was not significant after Bonferroni correction (table 3b, figure 2). Both brown and yellow parts of the breast were more saturated during the favorable year (table 3b, figure 3). No significant inter-annual differences were observed for the brightness of the brown or the yellow parts of this ornament (table 3b, figure 4). The differences that remained significant after Bonferroni correction ranged from moderate to large (table 3b, figures 2, 3).

The orange reflecting part of the beak spot exhibited a higher hue and a higher brightness during the favorable year, with moderate to large inter-annual differences (table 3b, figures 2, 4). No significant differences were observed for the orange saturation of this ornament after Bonferroni correction, and the effect size statistics suggested only a small inter-annual difference (table 3b, figure 3). Finally, the brightness of the UV reflecting part of the beak spot was slightly higher during the favorable year, though a small effect at best. No other significant differences were observed, and the effect size statistics suggested only null to small effects (table 3b, figures 2, 3, 4).

Table 3a. Inter-annual differences in the mean values (± s.e.) of hue, saturation, brightness, and morphometric measures of the auricular patch in each sex, and effect size statistics of the differences with their 95% confidence interval. *Welch's t test; §Student's t test; d.f.: degrees of freedom; in bold: significant differences after Bonferroni correction. See methods for statistical details.

			mean ± s.e.	t	d.f.	P-value	robust d [95% C.I.]
hue	males	2008	535 ± 2.0	3.4*	140.7	**0.0007**	0.34 [0.10 : 0.55]
		2010	527 ± 1.5				
	females	2008	525 ± 1.9	0.8*	136.5	0.4	0.03 [0 : 0.30]
		2010	523 ± 1.4				
saturation	males	2008	2.49 ± 0.038	8.4*	139.0	< **0.0001**	0.76 [0.61 :0.89]
		2010	2.08 ± 0.029				
	females	2008	2.33 ± 0.036	6.5*	137.5	< **0.0001**	0.63 [0.45 : 0.78]
		2010	2.03 ± 0.027				
brightness	males	2008	11.7 ± 0.39	-0.6§	153	0.5	0.06 [0 : 0.28]
		2010	12.0 ± 0.36				
	females	2008	13.2 ± 0.41	0.5§	153	0.6	0.14 [0 : 0.38]
		2010	12.8 ± 0.42				
auricular width (mm)	males	2008	42.1 ± 0.41	11§	153	< **0.0001**	0.88 [0.77 : 0.96]
		2010	36.5 ± 0.35				
	females	2008	38.5 ± 0.49	8.1*	129.3	< **0.0001**	0.79 [0.62 : 0.88]
		2010	33.6 ± 0.34				
inter-auricular distance (mm)	males	2008	35.1 ± 0.56	0.9§	153	0.4	0.12 [0 : 0.33]
		2010	34.4 ± 0.57				
	females	2008	38.5 ± 0.65	1.3*	135.6	0.2	0.16 [0 : 0.38]
		2010	37.4 ± 0.47				

Table 3b. Inter-annual differences in the mean values (± s.e.) of hue, saturation, and brightness of the breast patch and of the beak spot, and effect size statistics of the differences with their 95% confidence interval. *Welch's t test; §Student's t test; d.f.: degrees of freedom; in bold: significant differences after Bonferroni correction. See methods for statistical details.

			mean ± s.e.	t	d.f.	P-value	Robust d [95% C.I.]
breast patch - brown	hue	2008	579 ± 1.2	2.5§	308	0.01	0.25 [0.08 : 0.40]
		2010	575 ± 1.1				
	saturation	2008	2.74 ± 0.027	11.8*	257.7	< **0.0001**	0.78 [0.69 : 0.86]
		2010	2.35 ± 0.018				
	brightness	2008	11.4 ± 0.26	2.1§	308	0.03	0.14 [0 : 0.30]
		2010	10.7 ± 0.22				
breast patch - yellow	hue	2008	493 ± 0.61	-5.7§	308	< **0.0001**	0.41 [0.25 : 0.55]
		2010	498 ± 0.49				
	saturation	2008	1.84 ± 0.009	9.7*	279.2	< **0.0001**	0.68 [0.56 : 0.78]
		2010	1.73 ± 0.007				
	brightness	2008	28.8 ± 0.42	1.4§	308	0.2	0.11 [0 : 0.27]
		2010	28.1 ± 0.36				
beak spot - ultraviolet	hue	2008	386 ± 0.74	2.6§	308	0.01	0.18 [0.02 : 0.33]
		2010	383 ± 0.72				
	saturation	2008	0.73 ± 0.013	-1.1§	308	0.3	0.13 [0 : 0.27]
		2010	0.75 ± 0.011				
	brightness	2008	46.7 ± 0.79	2.9§	308	**0.004**	0.21 [0.05 : 0.37]
		2010	43.7 ± 0.66				
beak spot - orange	hue	2008	558 ± 0.35	6.3*	307.4	< **0.0001**	0.57 [0.43 : 0.69]
		2010	555 ± 0.39				
	saturation	2008	0.69 ± 0.008	2.4*	275.5	0.02	0.20 [0.03 : 0.38]
		2010	0.66 ± 0.006				
	brightness	2008	58.5 ± 0.79	5.2§	308	< **0.0001**	0.39 [0.2 : 0.52]
		2010	53.3 ± 0.64				

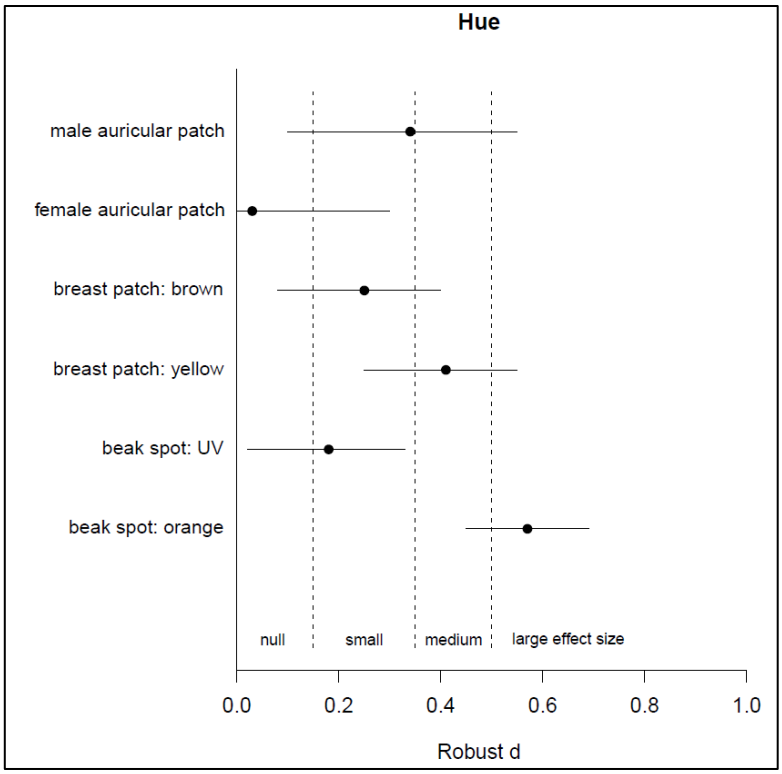

Figure 2. Effect size statistics of inter-annual differences in hue of color ornaments. Vertical dashed lines indicate the separation between null (< 0.15), small (< 0.35), medium (< 0.50), and large (> 0.50) effect size according to the Robust d criterion (see methods for statistical details).

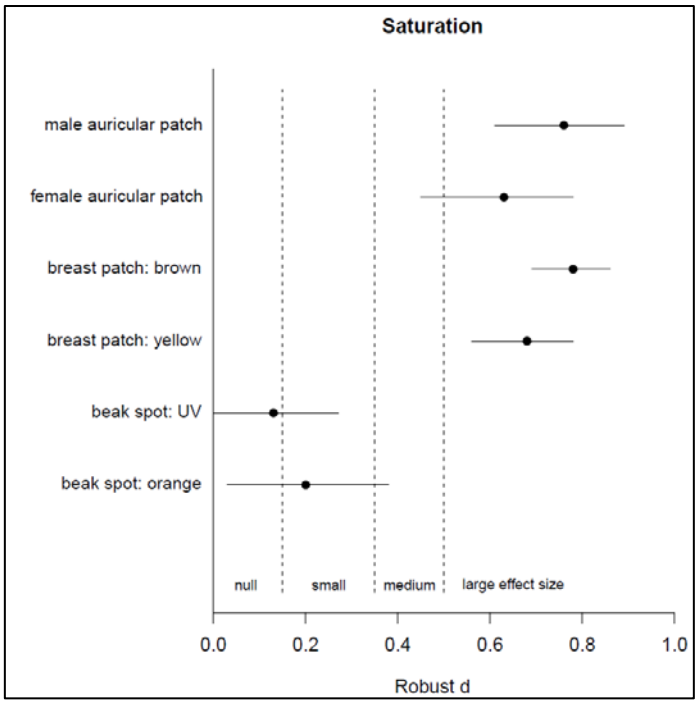

Figure 3. Effect size statistics of inter-annual differences in saturation of color ornaments. Vertical dashed lines indicate the separation between null (< 0.15), small (< 0.35), medium (< 0.50), and large (> 0.50) effect size according to the Robust d criterion (see methods for statistical details).

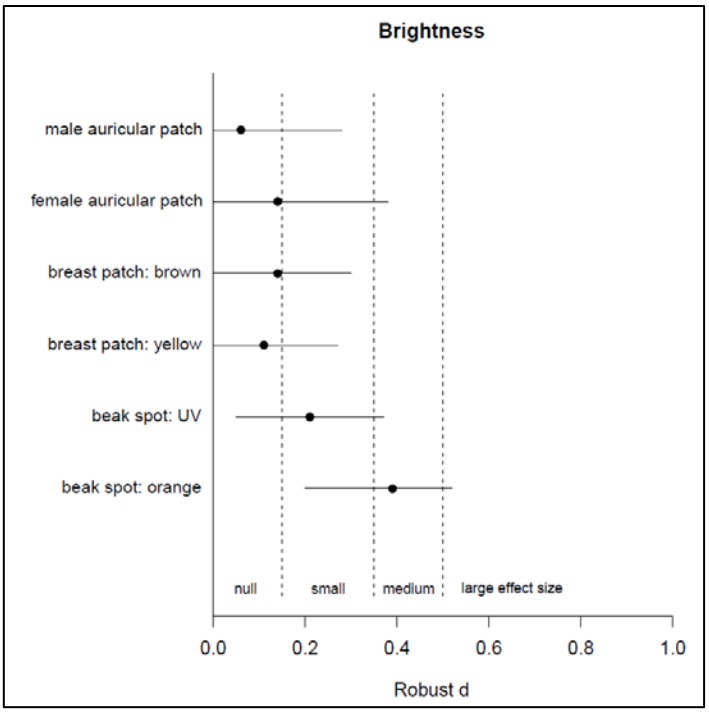

Figure 4. Effect size statistics of inter-annual differences in brightness of color ornaments. Vertical dashed lines indicate the separation between null (< 0.15), small (< 0.35), medium (< 0.50), and large (> 0.50) effect size according to the Robust d criterion (see methods for statistical details).

Variables influencing the pairing process of males and females each year

During the favorable year, no variables were found to significantly influence the pairing status, temporary versus definitive, of males (all P > 0.18). Significant differences were found between females involved in definitive pairs and females involved in temporary pairs for the UV hue (P = 0.0027) and for the orange hue (P = 0.032) of their beak spots. UV hue of the beak spot of females involved in definitive pairs was on average 6 nm lower than UV hue of the beak spot of females involved in temporary pairs (mean UV hue ± s.e. = 383 nm ± 1.4 and 389 nm ± 1.7, respectively), and quantification of this difference suggested a strong effect (robust d = 0.50; 95 % C.I. = [0.17 : 0.71]). Orange hue of the beak spot of females involved in definitive pairs was on average 2 nm lower than orange hue of the beak spot of females involved in temporary pairs (mean orange hue ± s.e. = 558 nm ± 0.63 and 560 nm ± 0.85, respectively); the 95% confidence interval of the effect size statistic reached 0.00, suggesting an null difference (robust d = 0.25; 95 % C.I. = [0.00 : 0.56]).

During the unfavorable year, no variables were found to significantly influence the pairing status of females (all P > 0.08). Significant differences were observed between males involved in definitive pairs and males involved in temporary pairs for their inter-auricular distance (P = 0.021) and for the orange hue of their beak spots (P = 0.022). Inter-auricular distance was slightly shorter for males involved in definitive pairs than for males involved in temporary pairs (mean ± s.e. = 33.5 mm ± 0.78 and 35.3 mm ± 0.82, respectively), and orange hue of the beak spot of males from definitive pairs was on average 2 nm higher than orange hue of the beak spot of males from temporary pairs (mean ± s.e. = 556 ± 0.83 and 554 ± 0.77, respectively). Both of these differences were found to be null according to the effect size statistic (inter-auricular distance: robust d = 0.23; 95% C.I. = [0.00 : 0.52]; orange hue: robust d = 0.24; 95% C.I. [0.00 : 0.54]).

Proportion of definitive versus temporary pairs, and inter-annual differences in the delay to egg laying

During the favorable year, 36 pairs (49 %) were temporary ones and 37 pairs (51 %) were definitive ones. During the unfavorable year, 39 pairs (48 %) were temporary ones and 43 pairs (52 %) were definitive ones. No inter-annual differences were observed for the proportion of temporary and definitive pairs ($chi^2 = 0.003$, d.f. = 1, P = 0.95).

Comparison of the latency to produce an egg revealed significant effects between years (z = 2.8, P = 0.005), as did pairing status (z = 7.1, P < 0.0001). Individuals that separated from their temporary mate took a shorter time to find a new mate and produce an egg during the unfavorable year than during the favorable year (mean delay ± s.e. = 13.7 days ± 1.1 and 17.8 days ± 1.9, respectively; figure 5). The same trend was observed for individuals involved in definitive pairs, although the size of the difference was much smaller (unfavorable year: mean delay ± s.e. = 8.6 days ± 0.25; favorable year: mean delay ± s.e. = 9.2 days ± 0.32; figure 5).

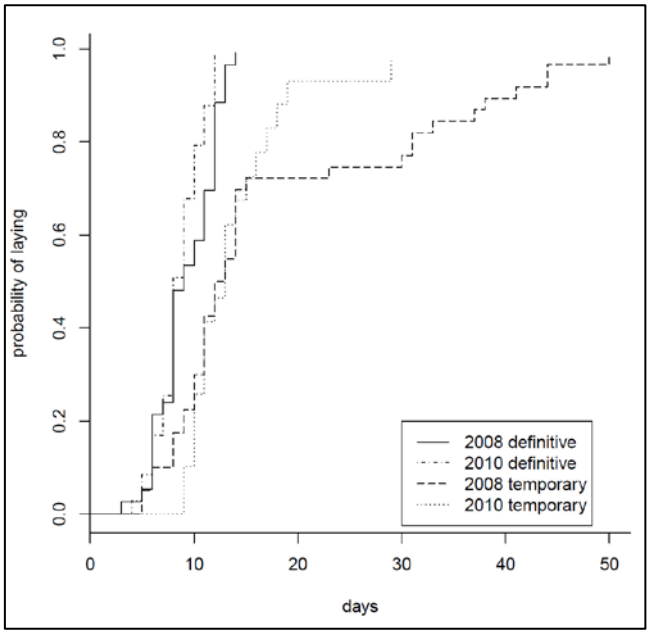

Figure 5. Probability of producing an egg for definitive pairs and of members involved into temporary pairs that found a new partner, during the favorable year and during the unfavorable year. Data include only pairs for which the laying date was known. See methods for statistical details.

5.4. Discussion

Main results

The aim of our study was to investigate inter-annual differences in body mass, color ornaments, and mating process in king penguins breeding during a year when marine resources availability were high and during a year when these resources were relatively scarce. Our first expectation that body mass should not greatly differ between years was supported in both sexes. Similarly, our second expectation that birds should express less conspicuous ornaments during the unfavorable year was also globally well supported. Our third expectation was that in both years, members involved in definitive pairs should express more conspicuous beak spots and males from those pairs should also express larger auricular patches. This was only partly and weakly supported, with females from definitive pairs expressing beak spots more UV in hue during the favorable year. Our fourth expectation was that ornaments which were found to influence the pairing success in previous studies should exhibit the lowest degree of inter-annual change. This last expectation was supported for UV color of the beak spot, but not for the size of male auricular patches. In addition females also expressed smaller auricular patches, although the size of the inter-annual difference was slightly smaller than the difference observed in males. Finally, we studied inter-annual differences in the proportion of birds involved in definitive and in temporary pairs each year, as well as the delay to lay an egg for each kind of pair. We observed a similar proportion of definitive and temporary pairs each year. Further, birds involved in temporary pairs took on average a shorter time to find a new mate and produce an egg during the unfavorable year, when we expected time to be short to the end of the breeding season, when chicks must overwinter while fasting on the beach.

No inter-annual differences in body mass

In both years, displaying individuals had a similar body mass. This result might seem surprising at first sight, because it would seem more intuitive that birds should be lighter during a year of poor resources availability. However, there is evidence that king penguins stop their breeding activities (courtship and incubation) when their body mass fall below a critical threshold: individuals entering in courtship with insufficient body reserves have to stop courting and return at sea to replenish their body reserves, and consequently produce their egg later with potential consequences on breeding success (Gauthier-Clerc et al. 2001). In addition, breeding adults must fast on the beach during incubation, as individual parents

regularly stand in the breeding colony with their egg on their feet for periods of about 15 – 21 days (Stonehouse 1960; Weimerskirch et al. 1992; Olsson 1996; Gauthier-Clerc et al. 2001; Descamps 2002). Thus, the lack of inter-annual differences in body mass observed in our study support the conclusion that there is a minimum body mass needed for successful reproduction. Birds with insufficient body reserves during the unfavorable year might have been forced to skip the reproductive season, as observed in the blue petrel *Halobaena caerulea* (Chastel et al. 1995). A long term monitoring of king penguin's breeding activity at the colony "La Grande Manchotière" (Crozet Archipelago) revealed a proportion of 7-19% non-breeders in the colony during the reproductive seasons of 1998 to 2005 (Le Bohec et al. 2007).

Inter-annual differences in color ornaments

Both sexes expressed smaller auricular patches and less strongly saturated feather ornaments during the unfavorable year, while the difference observed for the orange saturation of the beak spot was small. Recently, colors of ornamental feathers were found to be pterin-based and the orange color of the beak spot to be carotenoid-based (McGraw et al. 2004, 2007; Thomas et al. 2013). Moreover, saturation has been related to the concentration of pterins in Snares penguin colored feathers (McGraw et al. 2009), and to the concentration of carotenoids in mallard beaks (Butler et al. 2011). Thus from a mechanistically point of view, our results may suggest a lower allocation of pterins to feather ornaments during the unfavorable year, while maintaining the carotenoids allocation to the beak spot nearly constant. Carotenoid-based colorations rely on exogenous intake of pigments from food (McGraw 2006a, and references therein), while pterins are endogenously synthesized (McGraw 2006b, and references therein). Interestingly, both pigments are involved in immune and antioxidant functions, although the antiradical power of pterins has been found to be lower than that of carotenoids (Martinez & Barbosa 2010). Hence in king penguins, a potential complex environment-dependent trade-off between the amount of each pigment allocated to color ornaments and to immune and/or antioxidant functions might be at stake. For example when birds are under resources stress, allocating more pterins to the antioxidant function might allow a lower allocation of carotenoids to this function and a higher allocation to the beak spot, but perhaps at the cost of greater oxidative damage from free radicals. This example remains purely speculative, but suggests nonetheless interesting avenue for future research.

The changes in saturation that we observed related to different degrees of change in hue, depending on the trait considered. From the point of view of visual ornament production for communication, this suggests the existence of complex and trait-dependent mechanisms between produced and received visual signals. The most striking change was observed for the yellow hue of male auricular patches, which decreased by on average 8 nm during the unfavorable year while females exhibited only a slight and non-significant change (in addition this sex effect was also observed for the size and saturation, although to a much smaller extent). Potentially, this sex effect could be related to a higher constrain on resources allocation in males, as they virtually always take the first incubation shift (see introduction). Actual knowledge of color discrimination in king penguins, however, remain limited (but see Capuska et al. 2011); while predictive correlations could be drawn from existing microspectrophotometric data and physiological models for many terrestrial diurnal birds, deep-diving birds have different visual systems which make this approach slightly controversial for the moment (Hart & Vorobyev 2005).

According to our fourth expectation, we should have seen little inter-annual changes in UV color of the beak spot as well as in size of male of auricular patch. Our expectation was supported for UV color of the beak spot, but not for the size of male auricular patches. Due to the different nature of these two ornaments (structural and pigmentary, respectively), investigating the environmental sources and costs of ornament production for the several ornamental features of king penguins should prove a fruitful avenue of future research.

Inter-annual differences in the mate choice process

During the favorable year, we observed that females involved in definitive pairs expressed beak spots that were more UV in hue (i.e., reflected toward shorter wavelength) than females in definitive pairs. This effect, however, was not observed in males. In addition, we found no evidences that male auricular patch size influenced their probability to be involved in temporary or definitive pairs. Thus our third prediction was only supported in females during the favorable year. This result has been discussed in an extensive comparison of pairs that stayed together and pairs that separated during the favorable year (Keddar et al. unpublished data), so we will only briefly describe the main points of our argument. An essential step of the pairing process is call learning (Jouventin 1972), and we proposed that future work should distinguish phenotypic selection occurring before call learning and phenotypic selection occurring after call learning. In our colony, mate competition is biased toward males (Keddar et al. 2013). Thus, we suggested that females are highly choosy of the

male whose call they learn, while males would rather secure a first mate and switch to a better option only if they have the opportunity. Finally, we suggested that following individuals of both sexes through the entire pairing process should allow tests of our hypothesis. Interested readers are invited to consult Keddar et al. (unpublished data) for more details.

Focusing on inter-annual differences, we found evidence of male mate choice for UV beak ornaments of females during the favorable year, but no evidences of mate choice in either sex during the unfavorable season. In addition, birds that separated took on average less time to find a new mate and lay an egg during the unfavorable year that during the favorable year. Taken together, these results echo the growing literature on changing influences of sexual selection over time (see Cornwallis & Uller 2010 for a recent review). For example, in the lark bunting *Calamospiza melanocorys* (Chaine & Lyon 2008) and in the superb fairy-wren *Mallurus cyaneus* (Cockburn et al. 2008), the strength of sexual selection was undetectable in some years or acted in one direction one year and in the opposite direction in another. Moreover, in the collared flycatcher *Ficedula albicoris*, Robinson et al. (2012) found heritable differences in different years for female tendency to mate with highly ornamented males, and the fitness benefits associated with such mating depended on environmental conditions. In these three species, female mate choice appeared to be the strongest evolutionary influence on these temporal changes (Chaine & Lyon 2008; Cockburn et al. 2008; Robinson et al. 2012).

A potential explanation for the inter-annual differences in our results would be that the globally lower conspicuousness of ornaments expressed during the unfavorable year heightened the cost of sampling potential mates, as the most attractive ones were relatively rare (Jennions & Petrie 1997). Consequently, both sexes lowered their choosiness, which allowed them to pair faster and produce their egg as early as possible. In this way birds could partly compensate the initial delay with which they entered in reproduction during the unfavorable year. In a 55-year survey focused on Antarctic birds, Barbraud and Weimerskirch (2006) observed a significant shift of on average 9 days toward later arrival at the colony in response to climate change. Interestingly, this shift toward later arrival was accompanied by a shift toward later egg laying of only 2 days, suggesting a shorter pre-laying period (territory settlement and courtship). It is not known, however, what role sexual selection played in such shifts. In king penguins, the shorter pre-laying period that we observed could allow a partial adjustment of phenology to changing climatic conditions. But as emphasized in a recent review by Candolin and Heuschele (2008), such adjustment may be not sufficient to prevent

the strong decline of the populations predicted under forecasts of future Sub-Antarctic oceanographic conditions (Peron et al. 2012).

5.5. References

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APPENDIX A: Variance of color measures and morphometric measures of the auricular patch during the favorable year (2008) and during the unfavorable year (2010). Statistical differences were tested with F tests.

			variance	$F_{72,81}$	P-value	difference (%)
hue	males	2008	277	1,44	0,11	31
		2010	192			
	females	2008	263	1,61	0,04	38
		2010	163			
saturation	males	2008	0,107	1,51	0,07	34
		2010	0,071			
	females	2008	0,093	1,57	0,05	35
		2010	0,060			
brightness	males	2008	11,3	1,09	0,72	8
		2010	10,4			
	females	2008	12,3	0,85	0,47	16
		2010	14,6			
auricular width (mm)	males	2008	12,2	1,21	0,40	17
		2010	10,1			
	females	2008	17,8	1,93	0,004	48
		2010	9,2			
inter-auricular distance (mm)	males	2008	22,9	0,87	0,54	13
		2010	26,4			
	females	2008	30,5	1,65	0,03	39
		2010	18,5			

APPENDIX B: Variance of color measures of the breast patch and of the beak spot during the favorable year (2008) and during the unfavorable year (2010). Statistical differences were tested with F tests.

			variance	$F_{145,163}$	P-value	difference (%)
breast patch - brown	hue	2008	200	0,93	0,66	7
		2010	215			
	saturation	2008	0,110	1,99	< 0.0001	50
		2010	0,055			
	brightness	2008	10,2	1,32	0,08	25
		2010	7,7			
breast patch - yellow	hue	2008	54,3	1,36	0,06	27
		2010	39,9			
	saturation	2008	0,012	1,52	0,009	33
		2010	0,008			
	brightness	2008	26,2	1,20	0,25	17
		2010	21,8			
beak spot - ultraviolet	hue	2008	80,3	0,94	0,7	6
		2010	85,5			
	saturation	2008	0,025	1,27	0,14	20
		2010	0,020			
	brightness	2008	90,0	1,28	0,15	21
		2010	71,5			
beak spot - orange	hue	2008	18,1	0,72	0,048	28
		2010	25,0			
	saturation	2008	0,008	1,60	0,004	38
		2010	0,005			
	brightness	2008	91,2	1,34	0,07	25
		2010	68,2			

6. Conclusion

6.1. Discussion générale

6.1.1. Combats entre mâles et traits à double utilité

Nous avons observé que les combats entre rivaux du même sexe pour l'accès au partenaire étaient beaucoup plus fréquents chez les mâles que chez les femelles. Ce patron correspond à ce qui est observé classiquement chez les espèces présentant un degré de dimorphisme sexuel plus important, et pourrait expliquer la taille corporelle plus importante des manchots royaux mâles : chez un certain nombre d'espèces en effet, les mâles ayant une taille corporelle plus importante sont de meilleurs combattants et acquièrent une femelle plus facilement (Andersson 1994, p. 139-142).

Les manchots royaux mâles expriment également des patches auriculaires plus larges que les femelles. Lors de la défense du territoire, les mâles comme les femelles exprimant les patches les plus larges sont les plus agressifs, ce qui suggèrerait que ce trait joue le rôle de badge de statut (Cote 2000 ; Viera et al. 2008). La fonction de ce trait lors des affrontements entre mâles reste à élucider ; néanmoins, son dimorphisme sexuel et la fréquence des affrontements que nous avons observés pourraient suggérer qu'il joue également le rôle de badge de statut dans ce contexte.

Des expériences antérieures ont consisté à réduire la taille de ces patches chez les mâles et chez les femelles (tout en restant dans la gamme de variation naturelle), et à observer le délai nécessaire à chaque sexe pour trouver un partenaire de reproduction ; il a été observé que les mâles dont la taille des patches avaient été réduite mettaient plus de temps à s'apparier que les mâles dont les patches étaient intacts, et que la réduction de la taille de cet ornement était sans effet chez les femelles. Ces résultats ont été interprétés comme une évidence de l'existence d'un choix de la part des femelles pour les mâles exprimant les ornements les plus développés, et d'une absence de choix pour ce trait de la part des mâles (Pincemy et al. 2009 ; Nolan et al. 2010). Cependant la méthodologie employée ne permet pas de mettre formellement en évidence l'existence d'un choix de la part des femelles, et des explications alternatives sont possibles. A la lueur de nos résultats par exemple, le délai observé pourrait simplement résulter du fait que les mâles dont les ornements sont réduits rencontrent plus de difficultés à acquérir une femelle en raison d'une exposition plus importante aux agressions de leurs rivaux. Chez le souimanga de Johnston (*Nectarinia johnstoni*) par exemple, les mâles dont la taille des patches pectoraux a été expérimentalement réduite subissent plus

d'agressions et monopolisent moins de ressources (Evans & Hatchwell 1992 ; voir introduction).

L'explication alternative que nous apportons aux résultats de Pincemy et al. (2009) et à ceux de Nolan et al. (2010), toutefois, ne disqualifie pas la leur. Une conciliation est même possible en envisageant cette question sous l'angle des traits à double utilité (Berglund et al. 1996). En exprimant un choix pour les mâles ayant les patches auriculaires les plus développés, les femelles s'apparieraient dans le même temps avec un partenaire plus agressif. L'appariement avec un partenaire plus agressif pourrait permettre d'acquérir et de défendre un territoire de meilleure qualité (Cote 2000 ; Viera et al. 2008), et de bénéficier ainsi d'un succès reproducteur plus élevé. S'il semble que les deux sexes investissent autant l'un que l'autre dans la défense du territoire, la question de son acquisition reste néanmoins ouverte. Chez la Starique cristatelle (*Aethia cristatella*), un système présentant quelques similarités avec celui proposé ci-dessus semble être à l'œuvre. La Starique cristatelle (*Aethia cristatella*) est un oiseau marin nichant dans l'hémisphère nord. Les deux sexes de cette espèce possèdent une crête de taille similaire à la base de leur bec. Dans une première série d'expériences, Jones et Hunter (1993) se sont attachés à étudier le rôle joué par cette crête dans le processus de choix de partenaire. Ils ont présenté des modèles empaillés représentatifs de chaque sexe dont la crête avait été expérimentalement allongée ou raccourcie (en restant dans la gamme de variation naturelle) à des individus du sexe opposé, et ont observé que les modèles dont la crête était allongée recevaient plus de parades que les modèles dont la crête était raccourcie. Dans une seconde série d'expériences, Jones et Hunter (1999) se sont attachés à étudier le rôle joué par cette crête dans la régulation des interactions agonistiques. Ils ont à nouveaux utilisé des modèles empaillés dont la structure ornementale avait été allongée ou raccourcie mais les ont cette fois-ci présentés à des individus du même sexe que le modèle ; ils ont observé que les modèles dont la crête était allongée recevaient moins de réponses agressives. Leurs résultats suggèrent fortement que chez la starique cristatelle, la crête joue le rôle d'ornement sexuel et de badge de statut chez les deux sexes. Les conséquences de cette préférence mutuelle sur l'acquisition et la défense du territoire, cependant, restent inconnues ; et d'une manière générale, cette question est encore largement inexplorée chez les oiseaux marins.

6.1.2. Choix mutuel du partenaire

Le principal résultat du chapitre 3 supporte les précédentes études suggérant une implication du signal ultraviolet porté par l'ornement du bec dans le choix mutuel du partenaire. De récents travaux montrent qu'une coloration ultraviolette plus importante chez les femelles est corrélée au temps qu'elles investissent dans les soins au poussin (V. A. Viblanc, données non publiées), et donc un signal potentiel de leur qualité parentale. Cette qualité pourrait être également signalée de la même manière chez les mâles, mais des observations supplémentaires sont nécessaires pour en avoir la certitude. Chez le manchot antipode (*Megadyptes antipodes*), l'intensité de la coloration rouge des yeux et de la coloration jaune des plumes est corrélée à la qualité des parents (estimée par le succès reproducteur ; Massaro et al. 2003).

Les travaux conduits jusqu'alors avaient étudié l'influence des ornements sur le succès d'apparient en capturant des oiseaux n'ayant pas encore appris le chant de leur partenaire (Jouventin et al. 2008 ; Pincemy et al. 2009 ; Nolan et al. 2010), tandis que ceux présentés dans ce manuscrit se sont focalisés sur le choix de partenaire après l'apprentissage du chant. Ainsi, les résultats du chapitre 3 suggèrent que le processus de choix se poursuit après l'apprentissage du chant. Actuellement, nous savons que le chant du manchot royal porte une signature individuelle (Jouventin 1982) permettant aux partenaires de se reconnaitre (Derenne et al. 1979) et de se retrouver lors du retour à la colonie après un voyage en mer (Lengagne et al. 1999). Nous ne savons pas, toutefois, si le chant transmet d'autres informations en dehors de cette signature ni s'il joue un rôle quelconque dans le processus d'acquisition du partenaire (tel *un indice de qualité* : voir introduction). Cet aspect du processus d'appariement a été évoqué au sein de notre équipe, et une approche multimodale de la sélection sexuelle devrait être développée et testée dans les années à venir.

La comparaison interannuelle des ornements colorés et du choix de partenaire a révélé de fortes différences : pendant l'année où les conditions environnementales étaient défavorables, les ornements ayant une base pigmentaire étaient globalement moins colorés, présentaient un degré de variance plus faible (Chapitre 5, annexes A et B) et aucune influence de ces traits colorés n'a été détectée sur le processus de choix du partenaire. Une explication potentielle serait que seuls les individus de meilleure qualité sont entrés en reproduction, limitant dans le même temps les opportunités de choix en rendant la discrimination entre les partenaires potentiels trop coûteuse (en termes de temps de prospection par exemple), voire impossible sur le plan sensoriel. L'absence de marquage individuel à long terme limite les interprétations ; l'utilisation de bagues alaires pour un suivi à long terme n'est pas possible car

ces dernières réduisent l'efficacité de la nage et impactent la survie des individus (Saraux et al. 2011). L'étude des variations interannuelles des ornements exprimés par des individus connus n'est possible qu'avec la mise en place d'un programme de transpondage tel que celui réalisé sur l'archipel de Crozet. Concernant notre programme de recherche, les premiers tests de poses de transpondeurs ont été initiés en 2011.

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7. Développements méthodologiques

7.1. Mesure des ornements

La mesure du patch de poitrine, tout d'abord, peut être améliorée. Les résultats présentés dans ce manuscrit ont été acquis en prenant les mesures à deux emplacements différents : au début du dégradé, et en bas du dégradé, dans le jaune pâle. Cette approche cependant présente deux faiblesses. Tout d'abord, la mesure dans la partie jaune pâle manque de précision car chaque expérimentateur ne discrimine pas les couleurs avec le même degré de sensibilité. Ensuite, parce que nous perdons l'information sur la manière dont le patch passe du marron au jaune ; d'après premières nos observations sur le terrain, certains individus présentent des patches s'étendant sur une plus grande surface que d'autre. Une manière de résoudre ces deux problèmes est de s'équiper d'une règle flexible et de prendre plusieurs points de mesure éloignés d'un centimètre le long de l'ensemble du dégradé, en s'arrêtant à un point déterminé à l'avance (figure 1). En plus d'obtenir une mesure plus riche de l'ornement, cette méthode devrait également permettre d'obtenir une estimation de la longueur du patch. Nous avons testé cette approche sur le terrain lors d'une seconde campagne, mais ces données n'ont pas encore été analysées.

La mesure de la forme des patches auriculaires peut également être améliorée. Les observations sur le terrain suggèrent un certain degré d'asymétrie chez la grande majorité des individus, ainsi qu'une certaine variabilité interindividuelle. La raison de ces variations et leur caractère adaptatif est inconnue. Une expérience préliminaire à l'aide de photographies standardisées pourra permettre d'obtenir quelques pistes de réflexion.

7.2. Analyse des données

7.2.1. Variables colorimétriques

La quantification des couleurs ornementales a été faite par le calcul de la teinte, de la saturation, et de la clarté dans l'ensemble des manuscrits présentés (respectivement *hue*, *saturation*, et *brightness* dans Montgomerie 2006 ; abrégées TSC dans la suite de cette discussion). Le manuscrit d'article présenté dans le troisième chapitre a été évalué par deux referees ; tous deux ont critiqué cette approche, et suggéré l'utilisation de modèles physiologiques de perception des couleurs. Si nous reconnaissons l'utilité de ces modèles et avons pour projet d'analyser nos données à leur lueur, nous pensons toutefois que l'approche TSC ne doit pas être complètement abandonnée pour le moment. Cette approche nous est

initialement apparue comme la plus judicieuse en raison de la définition : ainsi la teinte pouvait être reliée aux variations du signal visuel, et la saturation (négativement corrélée avec la clarté) à la quantité de pigment présente dans les plumes (chez le gorfou des Snares *Eudyptes robustus*, la saturation des plumes est corrélée à leur teneur en pigment : McGraw et al. 2009). Etant donné que le manchot royal exprime 3 ornements, cela pose cependant le problème de générer 15 variables présentant des degrés de corrélation divers. L'utilisation d'un modèle physiologique, en caractérisant chaque ornement à l'aide d'une seule variable représentée dans un espace colorimétrique permet d'alléger les analyses et de s'affranchir des problèmes de colinéarité (Endler & Mielke 2005). Et même si les informations relatives au système visuel des manchots sont incomplètes, l'emploi d'un modèle physiologique aviaire générique reste possible (Endler & Mielke 2005 ; Capuska et al. 2011).

Après réflexion, nous pensons que ces deux approches relèvent de deux questions différentes : le système TSC se focalise sur le signal émis, tandis qu'un modèle physiologique se focalise sur le signal perçu. Ces deux techniques ne sont donc pas à opposer, au contraire, mais à utiliser conjointement. Cela risque de générer un volume de résultats important, mais en dernière instance la question de l'ornementation mutuelle se verra abordée dans le cadre de la communication visuelle d'une manière explicite, et ne pourra être que bénéfique pour notre compréhension du maintien des signaux extravagants du manchot royal.

Figure 1. Dégradé du patch de poitrine et règle flexible permettant de standardiser les points des mesures spectrophotométriques.

7.2.2. Installation du couple dans la colonie

Les résultats présentés dans le chapitre 4 relèvent d'observations préliminaires ; les questions relatives à l'acquisition et à la défense du territoire devront être approfondies lors des prochaines campagnes de terrain. Concernant la défense du territoire, la priorité sera d'établir un design statistique approprié. En effet, l'approche que nous avons employée ne prend en compte qu'une dimension spatiale (l'axe est-ouest de la colonie : voir la figure 1 du chapitre 4) et une analyse géostatistique plus fine en deux dimensions (axe est-ouest et axe nord-sud) pourrait mettre en évidence un patron de corrélation spatiale différent. Ce type d'analyse, cependant, nécessite une taille d'échantillon conséquente afin d'obtenir une puissance statistique suffisante et il faudra déterminer le ratio optimal entre taille d'échantillon et surface surveillée. Concernant l'acquisition du territoire, nous savons déjà qu'elle a lieu lorsque les couples sont formés (Stonehouse 1960 ; Weimerskirch et al. 1992 ; Descamps et al. 2002). Si nous savons également que les deux sexes semblent jouer un rôle similaire dans la défense du territoire (Cote 2000 ; Viera et al. 2008), des différences peuvent potentiellement exister quant au choix du territoire et au comportement agressif de chaque sexe lors de son acquisition. Des mesures et des suivis de couples lors de l'établissement du territoire permettront d'élucider cette question.

Les manchots royaux comme les manchots empereurs incubent leur œuf directement sur leurs pattes, et possèdent donc encore un certain degré de mobilité même une fois installé au sein de la colonie (les parents se déplacent d'en moyenne 4 mètres entre la ponte et l'émancipation thermique du poussin : Lengagne et al. 1999). Deux dynamiques d'interactions sont donc à l'œuvre : la première lors de la phase de recherche et d'acquisition du territoire, pendant laquelle les individus sont très mobiles et le taux de rencontre entre rivaux inconnus est élevé, et la seconde lorsque les individus sont établis au sein de la colonie et le taux de rencontre entre rivaux inconnus est plus faible, mais toujours présent. Potentiellement, ces deux dynamiques pourraient mettre en jeu des ornements différents. Dans tous les cas, la compétition pour les territoires semble à première vue sous-tendue par des mécanismes complexes.

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Le mot de la fin

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Finalement, une thèse ne se résume pas qu'au travail et ces trois ans ont été l'occasion de nombreuses rencontres inoubliables à Montpellier, à Kerguelen et en congrès. Si vous vous reconnaissez dans ces quelques mots, vous savez qu'il n'est pas nécessaire d'en dire plus...

A ma famille, à mes amis, et au tumulte de la vie.

Résumé

Si la sélection sexuelle proposée par Darwin fournit un cadre théorique satisfaisant pour expliquer l'évolution et le maintien des ornements sexuellement dimorphiques, le cas de l'ornementation mutuelle requiert l'emploi du cadre plus large offert par la sélection sociale. Dans de nombreux cas en effet, l'explication du maintien de l'ornementation mutuelle nécessite de considérer non seulement la compétition pour l'accès au partenaire de reproduction, mais également la compétition pour l'accès à d'autres types de ressources telles que la nourriture ou les emplacements pour nicher.

Cependant, le maintien de l'ornementation mutuelle n'est encore que partiellement compris chez les oiseaux marins. Les travaux réalisés au cours de cette thèse s'inscrivent dans la continuité des recherches initiées depuis quelques années dans le but de comprendre le maintien de l'ornementation mutuelle chez le manchot royal, un oiseau exprimant un patch orange présentant un pic de réflectance ultraviolet de chaque côté de la mandibule, des patches auriculaires jaunes de chaque côté de la tête et un patch formant un dégradé allant du marron au jaune pâle sur le poitrail. Les travaux présentés dans ce manuscrit de thèse portent (i) sur les combats entre individus du même sexe pour accéder à un partenaire de reproduction, (ii) sur le rôle des ornements colorés dans le processus d'appariement, (iii) sur l'association entre le degré de développement des ornements et la position du territoire occupé au sein de la colonie, et enfin (iv) sur l'existence de variations interannuelles concernant le degré de coloration des ornements et le processus de choix de partenaire. Les résultats révèlent que : (i) les affrontements pour l'accès au partenaire sont beaucoup plus fréquents chez les mâles que chez les femelles ; (ii) l'ornementation mutuelle du bec pourrait être maintenu pas le processus de choix mutuel ; (iii) les individus occupant les territoires les plus centraux de la colonie expriment des patches auriculaires plus large et un patch de poitrine plus coloré ; (iv) les ornements présentent des variations notables entre deux années, tout comme le processus de choix de partenaire. Pris dans leur ensemble, ces résultats révèlent que le maintien de l'ornementation mutuelle du manchot royal est multifactoriel, et des pistes de recherches sont proposées pour affiner notre compréhension de ce phénomène complexe.

Mots clés : écologie comportementale, sélection sociale, sélection sexuelle, ornements colorés, *Aptenodytes patagonicus*

Abstract

Darwin devised sexual selection theory in order to explain the evolution and maintenance of secondary sexual traits. In mutually ornamented species, however, the broader theoretical framework of social selection is needed. In many cases indeed, understanding the maintenance of mutual ornamentation requires to take into account competition for both sexual (i.e. mates) and non-sexual resources (e.g. food, nest sites).

How mutual ornaments maintain and evolve is actually not well understood in seabirds species. The aim of the research program within which this Ph.D. thesis took place was to understand the maintenance of mutual ornamentation in king penguin, a bird exhibiting a ultraviolet and orange beak spot on each side of the mandible, two yellow auricular patches, and a patch on the breast that grade from brown to bright yellow. We studied (i) same-sex fight over mates; (ii) mate choice for color ornaments; (iii) the relationships between conspicuousness of ornaments and position of the territory within the colony; and finally (iv) the existence of inter-annual variations in color ornaments expression and mate choice process. Our results show that: (i) same-sex fights over mates are highly male-biased; (ii) color of the beak spots may be involved in mutual mate choice; (iii) central individuals exhibit larger auricular patches and more colorful breast patch; (iv) ornament conspicuousness as well as mate choice show inter-annual changes. Taken together, these results reveal that maintenance of king penguin mutual ornaments is multifactorial, and some research avenues are suggested for future researches.

Key words : behavioral ecology, social selection, social selection, color ornaments, *Aptenodytes patagonicus*